HELSINGIN YLIOPISTO
HELSINGFORS UNIVERSITET
UNIVERSITY OF HELSINKI

The body length and community structure of cladocerans in lakes with variable concentrations of dissolved organic carbon

Faculty of Biological and Environmental Sciences

Department of Environmental Sciences

Environmental Change and Global Sustainability

University of Helsinki

Master's Thesis

Bernd-Niklas Mattila

April 2020

Tiedekunta - Fakultet – Faculty	Laitos - Institution - Department	
Bio- ja ympäristötieteellinen tiedekunta	Ympäristötieteiden laitos	
Tekijä - Författare - Author		
Bernd-Niklas Mattila		
Työn nimi - Arbetets titel - Title		
Vesikirppujen yksilökoot ja lajiyhteisöt vaihtelevissa järven liuenneen hiilen pitoisuuksissa		
Oppiaine - Läroämne – Subject		
Ympäristönmuutoksen ja globaalin kestävyyden maisteriohjelma		
Työn laji/ Ohjaaja - Arbetets art - Level	**Aika - Datum - Month and year**	**Sivumäärä - Sidoantal - Number of pages**
Pro gradu -tutkielma	huhtikuu 2020	53

Tiivistelmä - Referat – Abstract

Vesikirput ovat runsaita järvissä ja ovat tärkeitä hiilen ja energian kierrolle ravintoverkoissa. Ne ovat keskeisessä asemassa järvien ekosysteemeissä, mutta samalla ne ovat alttiina ympäristön muutoksille. Tutkimusten mukaan liuenneen hiilen (DOC) pitoisuus järvissä lisääntyy, joka puolestaan vaikuttaa moniin järven olosuhteisiin kuten ravinteiden ja valon määrään. Koska vesikirput ovat niin tärkeässä asemassa järvien ravintoverkoissa on tarpeellista tutkia, miten DOC pitoisuuden lisääntyminen järvissä vaikuttaa vesikirppuihin.

Tässä Pro Gradu työssäni tutkin miten vesikirppujen yksilökoot ja lajiyhteisöt erosivat toisistaan järvissä, joiden DOC pitoisuus vaihteli 2,4-33,5 mg l^{-1} välillä. Tätä tutkimusta varten nämä järvet jaettiin, joko kahteen ryhmään, joissa raja-arvona käytettiin 12 mg l^{-1} tai kolmen ryhmiin DOC pitoisuuksien mukaan. Tutkimuksen tuloksia verrattiin aiempaan tutkimusaineistoon vesikirppujen koosta. Näiden lisäksi tutkin miten järven DOC pitoisuus vaikutti kasviplanktonrunsauksiin tai lajiyhteisöihin, sekä muihin järven ominaisuuksiin, kuten veden väriin ja harppauskerroksen syvyyteen.

Tulokset osoittivat, että vesikirppujen keskikoko oli suurempi DOC pitoisuuden ylittäessä raja-arvon 12 mg l^{-1}. Muutokset vesikirppujen pituuksissa vaihtelivat heimojen välillä ja esim. Ceriodaphnia- ja Diaphanosomasukujen kirput olivat pienempiä niissä järvissä, joissa DOC pitoisuudet olivat korkeita. Bosminasuvun kirput puolestaan olivat suurempia korkeissa DOC pitoisuuksissa. DOC pitoisuuksilla ei ollut tilastollisesti merkitsevää vaikutusta vesikirppujen lajiyhteisöihin.

Tässä työssä tutkitut järvet vaihtelivat toisistaan DOC pitoisuuksien lisäksi ravinteiltaan, jonka takia järvien vertailu keskenään oli haastavaa. Tulokset osoittivat, että DOC pitoisuudet säätelevät eläin- sekä kasviplanktonyhteisöjä, mutta yksistään järven DOC pitoisuus ei riitä selittämään näiden vaihtelua. Vesikirput hyötyivät suuremmista DOC pitoisuuksista johtuen lähinnä DOC pitoisuuden ohella kohonneista ravinnepitoisuuksista. Vesikirppujen yksilökoon muutosten tulkitseminen oli vaikeaa, sillä vesikirppujen kokoon vaikuttavat useat tekijät sekä yksin että yhdessä.

Avainsanat – Nyckelord – Keywords

DOC -raja-arvo, ravinteet, klorofylli a, saalistus, kilpailu, ravintoverkot

Ohjaaja tai ohjaajat – Handledare – Supervisor or supervisors

Dr. Satu Estlander, Prof. Jukka Horppila

Säilytyspaikka - Förvaringsställe - Where deposited

Ympäristötieteiden laitos, Helsingin yliopisto

Muita tietoja – Övriga uppgifter - Additional information

Tiedekunta - Fakultet – Faculty	Laitos - Institution - Department	
Faculty of Biological and Environmental Sciences	Department of Environmental Sciences	
Tekijä - Författare - Author		
Bernd-Niklas Mattila		
Työnnimi - Arbetetstitel - Title		
The body length and community structure of cladocerans in lakes with variable concentrations of dissolved organic carbon		
Oppiaine - Läroämne – Subject		
Environmental Change and Global Sustainability		
Työn laji/ Ohjaaja - Arbetets art - Level	**Aika - Datum - Month and year**	**Sivumäärä - Sidoantal - Number of pages**
Master's Thesis	April 2020	53

Tiivistelmä - Referat– Abstract

Cladocerans play a key role in the aquatic ecosystem. They are abundant in lakes and are an essential part in the carbon and energy transfer of the food webs. These species are, however, prone to various environmental changes. Estimates have shown that dissolved organic carbon (DOC) concentrations in northern lakes are likely to increase in the future. This increase of DOC in lakes has multiple impacts ranging from nutrient levels to shading impacts reducing primary productions. Investigating changes in cladocerans along a DOC gradient could help us understand how these species might develop in the future in our changing climate.

In this Master's Thesis, I studied how the cladoceran body length and community structure varied between 9 lakes with dissolved organic carbon (DOC) concentration ranging from 2.4-33.5 mg l^{-1}. For the analyses, these lakes where divided into two groups with a threshold of 12 mg l^{-1} or into groups of three based on their DOC concentrations. Then, the results were compared with cladoceran length data from an earlier study. Additionally, the changes in phytoplankton abundances and communities as well as the relation between DOC concentration and other environmental variables were analysed.

The results showed an increase in the cladoceran body length above the DOC threshold. Moreover, the changes in body length varied between the studied genera. Both *Ceriodaphnia* sp. and *Diaphanosoma* sp. body length decreased in groups with higher DOC concentrations while *Bosmina* sp. were larger at high DOC concentrations. DOC concentration did not have any significant effect on the community structure of zooplankton.

The studied lakes varied from their environmental condition making comparisons and general statements challenging. The results indicated that DOC concentration regulates the planktonic communities, but it is solely an imprecise predictor for changes in zooplankton communities. However, cladoceran densities seemed to benefit from increased DOC concentrations as nutrient levels also increased. Changes in cladoceran body lengths were challenging to interpret, because there are multiple factors that can have an impact both alone and combined with others.

Avainsanat – Nyckelord – Keywords

DOC threshold, nutrients, chlorophyll a, predation, competition, food web

Ohjaaja tai ohjaajat – Handledare – Supervisor or supervisors

Dr. Satu Estlander, Prof. Jukka Horppila

Säilytyspaikka - Förvaringsställe - Where deposited

Faculty of Environmental Sciences, University of Helsinki

Muita tietoja - Övrigauppgifter - Additional information

TABLE OF CONTENTS

1 Introduction 5

1.1 Dissolved organic carbon and its origin 5

1.2 The impacts of DOC on the lake ecosystem 7

1.3 Cladocerans as part of the aquatic food webs 9

1.4 Bottom-up control of cladocerans 10

1.5 Top-down regulation by predators 11

1.6 The impacts of DOC on zooplankton 12

1.7 Research aim and hypotheses 15

2 Materials and methods 16

2.1 Study sites and zooplankton samples 17

2.2 Organizing the data and statistical analysis 19

3 Results 21

3.1 Changes in the community structure of zooplankton 21

3.2 Cladoceran body length 23

3.3 Impacts on phytoplankton communities 27

3.4 DOC and other environmental variables 28

4 Discussion 32

4.1 Factors affecting cladoceran length 32

4.2 Community structure of zooplankton 34

4.3 Impacts of DOC on the lake ecosystem and phytoplankton abundance 35

4.4 Challenges with the data and uncertainties 36

4.5 Looking into the future 37

5 Conclusions 38

6 Acknowledgements 39

7 References 40

8 Appendices 48

1 Introduction

Cladocerans, also known as water fleas, form a group of tiny aquatic species, barely visible to the naked eye, whose impact on the entire food web community structure and aquatic ecosystem is immense (Wetzel, 2001). Cladocerans are the bottom tier consumers that graze upon primary producers such as phytoplankton. They are abundant mainly in freshwaters, but some species can even inhabit marine areas. These aquatic animals are subject to various environmental changes that can affect their fitness and community structure. Therefore, it is important to research how these species might change and adapt to the future climate.

The amount of terrestrial dissolved organic matter (DOM) runoff into lakes has varied substantially in the past. According to the predictions, DOM runoff is likely to increase in the future along climate change as precipitation patterns change (Clark et al., 2010; Larsen et al., 2011a). This runoff can have various impacts on the lake such as increasing light attenuation which further affects lake temperature, oxygen levels and primary production (Morris et al., 1995; Williamson et al., 1996). Many of the DOM induced changes seem to occur in a non-linear way. For instance, according to Solomon et al. (2015) and the studies they refer to, sudden changes in the lake food webs can be observed once the dissolved organic carbon (DOC) concentrations exceed 10-14 mg l^{-1}. However, the mechanisms behind these changes and the complex ecological impacts have not been studied extensively. Because both cladocerans and DOC hold such key roles in the aquatic ecosystems, I will investigate in this Master's Thesis, whether the body length and community structure of cladocerans change across lakes with varying DOC concentrations and if some clear patterns can be found along this gradient.

1.1 Dissolved organic carbon and its origin

Terrestrial dissolved organic matter (DOM) consists of a vast variety of different organic substances that pass through a 0,45 µm filter (Thurman, 1985; Bolan et al., 2011). The largest fraction of DOM is in the form of dissolved organic carbon (DOC) (Mattsson et al., 2005). Other common substances are dissolved organic nitrogen and phosphorus (DON & DOP), carbohydrates, amino acids, and lignin derived phenols and aromatic hydrocarbons (McDonald et al., 2004; Minor et al., 2014). DOM can

also include amino sugars like N-acetylglucosamine (NAG), which is an important building block of the bacterial cell wall (Riemann & Azam, 2002). These substances are further altered by physical and biological processes that change their chemical structure leading to matter with varying molecular size and biological availability (Neff & Asner, 2001). Therefore, many of the DOM substances remain unidentified (Minor et al., 2014). Often when measuring DOM concentrations, it is only referred as DOC (Thurman, 1985; Bolan et al., 2011; Solomon et al., 2015). In this Thesis, I will be using DOC even though in some cases DOM would be the more accurate term.

Allochthonous DOC originates from the land and ends by runoff into the lakes. As rain falls and penetrates the surface of soil it goes through the vegetation, roots and different soil layers taking up all sorts of dust, gases, leaves and roots and soil microbial products. The largest part of DOC consists of plant material that has been decomposed to different extend (Thurman, 1985; McDowell & Likens, 1988; Wetzel, 2001). The amount of DOC runoff depends on many factors, including temperature, precipitation, vegetation and soil properties such as pH and redox potential that regulates the solubility of DOC and decomposition rates (Thurman, 1985). In general, hydrology is an important regulator of DOC concentration in lakes, because it works as a vector for transport and because the accumulation of organic matter in wet soils is faster than the mineralization leading to larger amounts of export (Freeman et al., 2001; Wickland et al., 2012). For example, the DOC runoff from peatlands is typically higher than from forest areas (Mattsson et al., 2005). Peatland DOC runoff is party controlled by temperature that regulates the extracellular enzyme activity. Seasonality is also an important factor in DOC runoff concentrations and especially the spring snow melts create DOC runoff spikes (McDowell & Likens, 1988; Wickland et al., 2012).

Autochthonous DOC is formed when primary producers emit photosynthesis products, cells are decomposed and through the sloppy feeding of zooplankton (Møller, 2005; Hansell & Carlson, 2014). Autochthonous DOC can be a major contributor of total DOC concentrations in shallow and eutrophic lakes that have high primary production rates.

DOC concentrations in lakes have increased in the past decades in north temperate and boreal regions (Hanson et al., 2007; Monteith et al., 2007). This increase in DOC concentration has led to the browning of these surface waters (Skjelkvåle et al., 2005; Roulet & Moore, 2006; Kritzberg & Ekström, 2012; Sanclements et al., 2012). It has been suggested that one of the primary drivers for this increase might be the decrease in atmospheric sulfate deposition which is the result of tighter

emission regulations (Monteith et al., 2007; Erlandsson et al., 2008; Clark et al., 2010). Sulfate deposition decreases soil pH and increases ionic strength which reduces the solubility of soil organic matter (Freeman et al., 2001; Clark et al., 2005; Monteith et al., 2007). Additionally, the changing precipitation patterns and temperatures of our changing climate will likely impact DOC runoff amounts today and in the future (Solomon et al., 2015).

1.2 The impacts of DOC on the lake ecosystem

Lakes are important for the local and global carbon cycle (Cole et al., 2007; Tranvik et al., 2009). The allochthonous carbon has a major role in the structure and function of a lake ecosystem (Jones, 1992; Williamson et al., 1999; Prairie, 2008). These impacts can be seen from the cellular levels of organisms to ecosystem biological cycles (Steinberg et al., 2006; Prairie, 2008). The influences occur either directly or indirectly through the changes in the physical environment of these lakes.

The DOC is also an energy input to the food webs (del Giorgio & Peters, 1994; Pace et al., 2004). The carbon is quickly consumed by heterotrophic bacteria and mineralized (Berggren et al., 2010). Some of the DOC is respired by the bacteria as CO_2, adding to the pool of CO_2 flux from water to the atmosphere (Hope et al., 1996; Sobek et al., 2003; Larsen et al., 2011b). These released nutrients and inorganic carbon are available for other primary producers and thus enhances the phytoplankton production. DOC is further incorporated into the bacteria cellular structures and becomes available to higher consumers like zooplankton and fish. Studies show that a major portion of the consumer biomass originates from terrestrial DOC inputs (Grey et al., 2001; Karlsson et al., 2003; Pace et al., 2004; Matthews & Mazumder, 2006; Cole et al., 2011; Tanentzap et al., 2014). Especially during the summertime, the organic nutrients can have a major impact when inorganic nutrients are low (Mattsson et al., 2005). DOC can thus have a key role in lake eutrophication.

DOC affects the physical state of the lake by being the primary regulator of water column transparency to shortwave energy (Morris et al., 1995; Williamson et al., 1996). The UV- and visible light absorbing fraction, chromophoric dissolved organic material (CDOM) absorbs sunlight and hinders the light uptake of autotrophs and thus constrains primary production to near surface-layers (Jones, 1992; Carpenter et al., 1998) (Fig. 1). This uptake of the visible light fraction gives lakes with high DOC concentrations its brownish colour (Jones, 1992). Moreover, as light is absorbed it changes

the vertical distribution of heat and light (Fee et al., 1996; Kirk, 2011). Light and temperature are some of the most important regulating factors in lakes, because they control metabolic rates, primary production, biochemistry and multiple other processes in the lake. Lakes with high DOC concentrations have higher near surface layer energy fluxes and are on average colder (Read & Rose, 2013). If there is not enough of mixing energy to prevent stratification then the thermocline is closer to the surface and more stable (Kling, 1988; Read & Rose, 2013; Palmer et al., 2014). The thermocline depth affects the vertical gradient of dissolved oxygen and other chemicals which impact biochemical reactions and habitat suitability for many organisms (MacIntyre et al., 2006; Imberger, 2011). Shallower stratification might also limit phytoplankton access to nutrients that have been internally recycled (Jones, 1992; Hessen, 1998; Jansson et al., 2012). The impacts of water quality on the thermal structure is often stronger in small than large lakes (Fee et al., 1996).

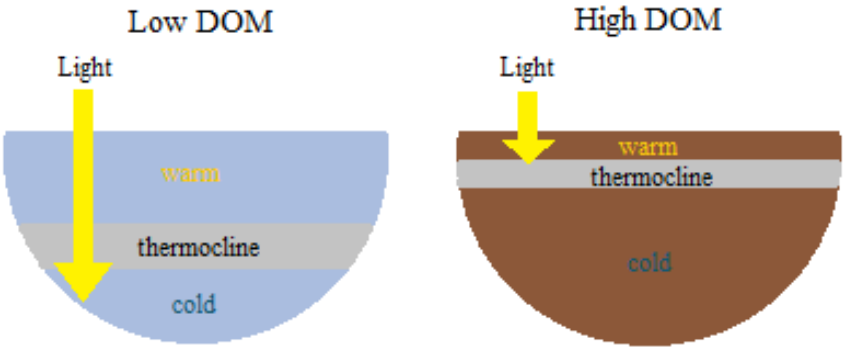


Figure 1.The light and temperature distribution depend on the DOM concentrations. In low DOM concentrations (left) the light penetrates the water column much deeper, warming the lake and increasing the thermocline depth. Lakes with high DOM concentrations (right) are overall colder and have a shallower thermocline depth.

There seem to be a non-linear relationship between DOC inputs and lake ecosystem processes (Solomon et al., 2015). Clearer lakes have enough light to enable primary production but are usually nutrient limited, whereas lakes with high DOC concentrations have plenty of nutrients, but the shading restricts the primary production. This threshold is suggested to be around 10-14 mg l^{-1} above which it negatively affects the primary and consumer production (Karlsson et al., 2009; Kelly et al., 2014). Bergström & Karlsson (2019) also showed that the phytoplankton biomass was the largest at DOC concentrations 11 mg l^{-1}, which is just within the suggested limits.

1.3 Cladocerans as part of the aquatic food webs

Food webs represent the feeding relationship of all trophic levels (Smith & Smith, 2015). These trophic relationships play a major role in structuring the aquatic food webs (McQueen et al., 1986). The aquatic food webs are further altered by numerous environmental factors such as DOC in complex ways (Kissman et al., 2017).

Species in the food web can be categorized into either 1) autotrophs, that can produce organic matter from inorganic substances e.g. phytoplankton or 2) heterotrophs, that consume other species to gain their energy. Food webs are regarded as interactions between organisms in which energy shifts from one level to another (Fig. 2). Typically, the intensity of bottom-up regulation is strong at the bottom of the food chain and attenuates toward higher levels. Top-down regulation is strong at the top and attenuates in the lower levels. Carpenter et al. (1987) states, that both grazing and abiotic factors can be equally potent regulators of primary production. However, the trophic cascade can sometimes affect the lake ecosystem significantly and at other times have very little or no effect.

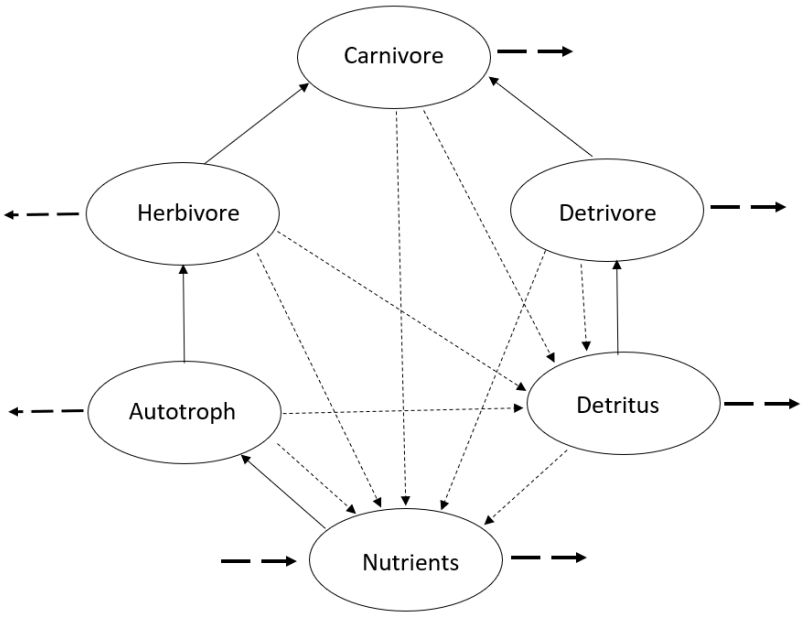


Figure 2. Schematic diagram of the food web. The solid arrows show the consumer–resource interactions and the dashed arrows represent the flow of nutrients from the living components to detritus or the nutrient pool. The bolded arrows illustrate the input of external nutrients and the losses of each food web component (Attayde & Ripa, 2008).

In the food web, zooplankton graze on phytoplankton or eat smaller zooplankton and are themselves food for fish and other higher trophic animals. In the food web theory the “paradox of plankton” is an interesting hypothesis (Hutchinson, 1961). It states, that the diversity of phytoplankton species is very large despite the homogeneity of their environment. The phytoplankton communities might change continuously and never stay in a steady state.

Cladocerans are zooplankton but more precisely they are arthropods that belong into the class Branchiopoda, forming one of the four monophyletic groups. Cladocerans are small, generally between 0.2–6.0 mm in body length and commonly have 4-6 limbs. Altogether, around 620 species have been described and it is likely, that many cladocera species remain undescribed (Forró et al., 2008). In Finland, the number of known cladocera is between 70-80 species of which most live in freshwater environments.

All cladocera species are heterotrophs, but their diet preferences differ (Irvine, 1986; Wetzel, 2001). Cladocerans such as *Bosmina* sp. and *Daphnia* sp. are grazers feeding mainly on phytoplankton, but the feeding apparatus is so efficient that it can even collect bacteria (Ebert, 2005). Larger cladoceran species such as *Leptodora kindtii* (Focke, 1844) and *Polyphemus pediculus* (Linnaeus, 1761) are predators feeding on smaller zooplankton. Cladocerans can have a major impact on food webs. For example, larger *Daphnia* sp. individuals have higher filtration rates which could increase top-down regulation (Burns, 1969; Peters & Downing, 1984). Furthermore, because of their key position in the food web, cladocerans have been used as indicators for environmental changes. Like other arthropods, the cladocera shed their exoskeleton during multiple stages in their lifecycle making them ideal for paleolimnological studies (Korosi et al., 2008).

1.4 Bottom-up control of cladocerans

The impacts of eutrophication on Bosminid abundances have been studied to understand how changes in nutrient loadings could affect the lake ecology (Liu et al., 2009; Brown et al., 2012; Nevalainen & Luoto, 2013). Eutrophication has been noticed to increase cladoceran biomasses and abundances as eutrophication intensified and to decrease following oligotrophication (Jeppesen et al., 2011; Guilizzoni et al., 2012). Higher nutrient fluxes enhance primary production that increases the availability of food for the zooplankton. However, these changes vary across cladoceran genera

and for example the changes in *Bosmina* sp. populations occurred usually before those in *Daphnia* sp. populations (Brown et al., 2012). Cladocerans have varying feeding behaviors and the feeding preferences might regulate the succession of phytoplankton communities and vice versa (Irvine, 1986; Wetzel, 2001). These feeding habits and preferences might also impact the body growth of cladocerans (Becker et al., 2004). It is also important to notice, that the dependence between zooplankton and phytoplankton biomasses do not occur simultaneously (McCauley & Kalff, 1981). Changes in phytoplankton biomasses and communities can be reflected in the zooplankton multiple days later and responses are slower the higher the trophic level.

The closer the ecological niche, the more there is competition between individuals. Typically, when food is scarce the larger individuals outperform smaller ones. The size efficiency hypothesis by Brooks & Dodson (1965) states that large zooplankton are more efficient consumers and outcompete smaller zooplankton if predation pressure is low. However, when the predation by planktivores increases, the small zooplankton prevail (Brooks & Dodson, 1965). As more food is available the need for competition over resources decreases leading to a decrease in average body length (Gliwicz, 1990). In the case of planktonic *Daphnia* sp. and *Bosmina* sp. the small individuals prevailed in higher nutrient-level lakes and large sized individuals in oligotrophic lakes (Korosi et al., 2008).

However, there are studies in which this theory is turned up-side down. In some cases small-bodied species outcompete larger rivals in low nutrient levels and vice-versa, the large cladocerans can dominate competition in abundant food situations (Romanovsky & Feniova, 1985). Aside from body size, the slowly growing individuals might also outcompete the fast growing species (Romanovsky, 1984).

1.5 Top-down regulation by predators

Going up the food chain we have fish and invertebrates that feed on zooplankton. The impacts of top-down predation can have various complex effects on the prey communities. Cladoceran body length and biomass has been observed to be higher under fish absence (Vanni, 1987). Moreover, in absence of fish the cladocerans were able to control the abundance of phytoplankton species upon which they graze indicating a trophic cascade effect in the food web. Large cladoceran individuals

tend to be noticed better by predators and end up easier as prey. Sommer & Stibor (2002) showed that fish prefer eating larger sized cladoceran individuals whereas smaller cladocerans are preyed upon by invertebrates (Liu et al., 2009; Korosi et al., 2013). High abundances of planktivore fishes such as cyprinids can affect both biomass and average body length of zooplankton. The high predation pressure by fish led to the decrease of Bosminid body length (Nevalainen & Luoto, 2013; Nykänen et al., 2010). Korosi et al. (2013) further suggested that high predation pressure might drive cladoceran communities towards smaller species and individuals. It can be argued, that instead of simple top-down regulation affecting only cladoceran biomass or body length the predations impacts are reflected in the cladoceran community dynamics.

The predation might also affect the morphology of cladocerans (Korosi et al., 2013; Sakamoto & Hanazato, 2008). These studies suggest that morphological traits such as antennule shape and appendage length might determine cladoceran vulnerability to copepod predation. Furthermore, seasonality can be a key factor affecting cladoceran densities and body size during summer (Liljendahl-Nurminen et al., 2003). The causes for changes during seasons can be diverse. For example, the cladoceran biomass peak and increased body length during mid- to late summer might be due to the relieved predation pressure from the Chaoborids (Liljendahl-Nurminen et al., 2003).

1.6 The impacts of DOC on zooplankton

There have been multiple studies investigating the role of DOC on the food webs and zooplankton with differing results. For example, food webs based on bacteria enable the allochthonous DOC for the consumers and the carbon becomes an important resource for zooplankton accounting for up to 70 % of their carbon utilization (Cole et al., 2011; Mitrovic et al., 2014; Tanentzap et al., 2017). Furthermore, cladoceran and copepod densities increased under elevated DOC concentrations as it fueled the food webs (Bowszys et al., 2014).

Some mesocosm studies did not find a significant relation between DOC and water colour towards zooplankton biomass and diversity (Lebret et al., 2018; Robidoux et al., 2015). However, it is possible that either the time span or concentrations were not sufficient for changes to occur. Other studies have shown that dark water reduces the abundance of zooplankton and zoobenthos that form the base of the food chain supporting fish (Karlsson et al., 2009; Jones et al., 2014; Kelly et al., 2014).

The negative impacts are commonly chained to the reductions in resource quality and habitat availability. However, further studies showed an increase of zooplankton densities as DOC concentration were increased from 8 to 11 mg l^{-1} in a manipulated lake study (Kelly et al., 2016). This was due to a significant increase in gross primary production and resource quality (lower seston carbon-to-phosphorus ratio). The increase of allochthonous DOC commonly raises the amount of available nutrients. This increases the abundance of phytoplankton which further stimulates the higher trophic levels of the food web such as the abundance of herbivorous zooplankton (McQueen et al., 1986; Power, 1992). Moreover, the abundance of cladocerans has been noticed to increase with higher nutrients and food availability (Nevalainen & Luoto, 2013; Sweetman & Finney, 2003).

DOC has another major impact on lakes. As light attenuation is stronger, the stratification during summer occurs at a shallower depths and the overall lake temperature decreases. During summer, the decomposition of organic matter and aerobic respiration consumes all the oxygen below the stratification level. This area becomes a refuge for animals with a lower oxygen demand (Larsson & Lampert, 2011). Most fish species require more oxygen and stay in oxygen rich water layers whereas many invertebrate predators tolerate low oxygen levels. Darkness, low oxygen concentrations and small body size give better opportunities for animals such as cladocerans to avoid fish predation (Shapiro, 1990; Larsson & Lampert, 2011). This is one of the causes for the diurnal vertical migration of cladocerans which migrate from deeper waters towards the surfaces as darkness approaches (Wetzel, 2001). In lakes with high DOC concentrations, the oxygen and temperature gradients are steeper, light penetration is shallower, the phytoplankton is limited to the surface and possibly also the threat posed by invertebrate predators increases in deeper water. Thus, the migratory patterns of cladocerans might change so that these remain in shallower water also during daytime (Wissel & Ramacharan, 2003). The study by Estlander et al. (2017) suggested that DOC concentrations might impact the diurnal behavior and habitat use of cladocerans. In less humic lakes the studied cladoceran species escaped predation by hiding under plants. However, in highly humic lakes the abundance was highest in free-swimming individuals regardless of daytime. Moreover, small cladocerans that are targeted by invertebrate predators located constantly higher in the water column compared to large cladocerans (Wissel & Ramacharan, 2003).

Light intensity can sometimes have a stronger effect on large prey than on small prey (Utne, 1997). The search time and reaction distance of a Goby feeding on copepods suggested that prey size affected reaction distance at all illumination levels, but size only impacted search time under low

light conditions (<300 lx) (Utne, 1997). The longer search time for smaller copepods indicated that the combination of small body size and poor visibility helped zooplankton avoid predation. Liljendahl-Nurminen et al. (2008) showed that a combination of physiological and visual strains decreased the predation pressure of fish on Chaoborus larvae. These changes in oxygen and turbidity had a more profound effect on the behavior of the fish than on their feeding efficiency. Additionally, the decreased predation pressure of fish could increase the impact of invertebrate predation on zooplankton in the metalimnon.

DOC and lake depth have been suggested as important predictors of cladoceran species assemblage (Korosi & Smol, 2011). For example, under high DOC concentrations the abundance of mud- and rock-associated taxa, such as the species *Monospilus dispar*, should be higher than that of vegetation related taxa (e.g. *Sida* and *Polyphemus*) due to the absence of macrophytes in highly coloured water. Under such conditions, the predation on cladocerans would shift from fish towards a more invertebrate dominated predator community which would favour large sized cladocerans. Contrary to the predictions, the study by Korosi & Smol (2011) observed shorter bosminid carapace and mucrone length in lakes with high DOC concentrations. These results indicated that nutrients might be more important in regulating bosminid size compared to DOC concentrations (Korosi et al., 2008; Korosi & Smol, 2011).

A meta-analysis on cladoceran body length concludes that it is a complex array of extrinsic environmental factors and biological intrinsic influences that are reflected in both direct functional and evolutionary impacts (Hart & Bychek, 2011). For example, Smith & Cooper (1982) showed that in addition to resources, inter- and intraspecies competition are the most important regulators of cladoceran population dynamics. Predation is important but has a subsidiary role at high nutrient levels, because the impacts of predation cannot control the zooplankton abundance. Thus, it can be concluded that several factors can regulate either alone or in combination, both directly and indirectly, the size and community of cladocerans.

1.7 Research aim and hypotheses

This Master's Thesis is part of the "Humuskuormituksen mittarit" (HUMI) project which is conducted in the Ecosystems and Environment programme of the University of Helsinki. The HUMI project aims to investigate the role of humic loading to adjacent waters. The results would promote water conservation policies and develop sampling techniques that could estimate the impacts of humic load on the lake ecosystems.

This Thesis aims to find out whether the data of the HUMI project shows similar trends of a DOC threshold as mentioned in Solomon et al. (2015) and if some of the mechanisms behind these changes could be explained. Therefore, to examine the factors behind the observed phenomenon, I explore the structure of the zooplankton community and the body lengths of cladocerans. Additionally, to get more validity to the observations of the HUMI data, I will compare my findings with the data collected for the earlier SUSFISH -project (SUSFISH; Sustainable fishing 2006-2013) where the research was focused on the communities of humic lakes and their predator-prey relationships.

The hypotheses of this thesis are:

- The zooplankton community structure will change abruptly once the DOC concentrations exceed a certain threshold (10-14 mg l^{-1}). Especially, the average body length of cladocerans are expected to change, because environmental changes are reflected in cladoceran body sizes.
- The phytoplankton community structure will change abruptly as the DOC concentration rises, because nutrients levels increase but light availability decreases.
- The chlorophyll a to phosphorus ratio of the studied lakes will decrease with increasing DOC concentration as shading impairs primary production.

2 Materials and methods

The data for this master's thesis was provided by the HUMI project and was collected in June-August 2019. The data includes three replicate samples of nutrient (TN and TP), DOC, Fe, suspended solids (SS) and chlorophyll a concentrations, water colour, chemical oxygen demand (COD) and light attenuation from 50 lakes in southern Finland (Appendix 1). The data also contains biological data on planktonic communities from 9 lakes in which the DOC concentration varied from below 3 mg l^{-1} to above 30 mg l^{-1}.

The DOC was analyzed by using a standard method SFS-EN 1484 (Shimadzu TOC 5000A analyzer) (Laine et al., 2014) and water colour was determined spectrophotometrically as the absorbance of light at 420 nm wavelength. Chlorophyll a was analyzed spectrophotometrically after filtering with GF&C filters and exctraction with ethanol (Holmroos et al., 2012). Total nitrogen (TN) and total phosphorus (TP) were determined using the method by Koroleff (1979) (Lachat autoanalyzer, QuickChem Series 8000). The concentration of suspended solids (SS) were determined according to SFS-EN 872 method and filtered through Whatman GF/C filters. At deepest part of each lake, Secchi disk depth was measured, profiles of dissolved oxygen, turbidity, pH, and temperature were measured with a YSI-6600 sonde (YSI). Light intensity was measured with a LI-1400 datalogger with quantum sensors (LI-COR Biosciences, Lincoln,NE, USA). Light attenuation coefficient was calculated from light intensity measurement from the surface (1 cm below water level) and at 1 m depth. Light attenuation was calculated by the formula:

$$l_z = l_0 e^{-kz}$$

where I_z is light intensity at depth z, I_0 intensity below the water surface, k attenuation coefficient, z depth.

Additionally, I analysed data sets from the SUSFISH -project that contained data on cladoceran body lengths from 6 lakes between the years 2007-2013. This data also includes nutrient (TP and TN) and chlorophyll a concentrations and water colour. The DOC concentration for these lakes were calculated using the water colour values (Molot & Dillon, 1997).

$$DOC = 1.514 + 0.090 * absorbance$$

2.1 Study sites and zooplankton samples

Sampled lakes situated in southern Finland and most of them in the Evo hiking area (Fig. 3). The zooplankton samples of the HUMI project were collected from 9 lakes with 3 replicates each for a total of 27 samples.

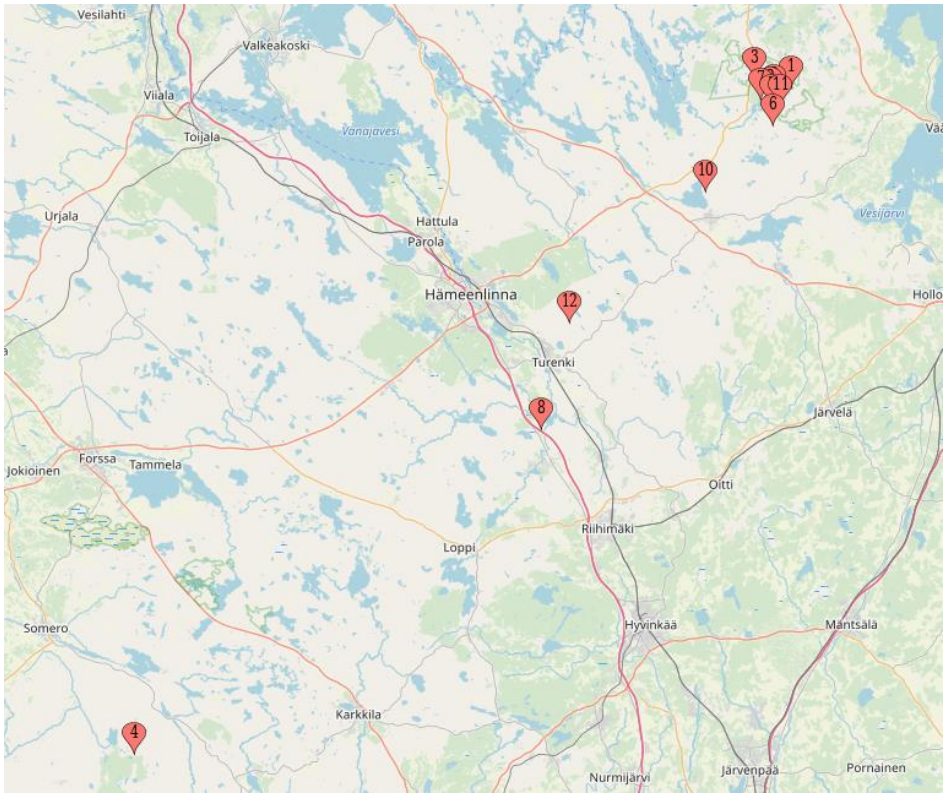


Figure 3. Samples sites: 1. Haarajärvi 2. Haukijärvi 3. Hokajärvi 4. Iso Valkjärvi (IVA) 5. Majajärvi 6. Syrjänalunen 7. Valkea-Mustajärvi 8. Kernaalanjärvi 9. Rahtijärvi 10. Kyynäröjärvi 11. Horkkajärvi 12. Käkilammi. SUSFISH samples (1-6), HUMI samples (4-12). (Map customizer, accessed 25.02.2020)

Zooplankton samples were taken from the deepest part of the lake with the 50 µm-mesh plankton net (25 cm opening), towed vertically through the water column from the 1m depth to surface. In each sampling site, three parallel plankton net hauls were taken and preserved with formaldehyde (CH_2O) and stored in the refrigerator (+ 4°C) (Fig. 4).

In the laboratory, zooplankton were enumerated, identified to genus level and cladoceran carapace length was measured using an inverted microscope with a 125x magnification (Olympus CKX41). The aim was to measure 30 individuals per genus for each of the 27 samples, but due to the low densities of some of these genera, the aim was not met for all genera (Appendix 3). For most genera the

length between the upper corner of the eye to the base of the tail spine was measured (Fig. 5). Similar methods have been used in other studies (e.g. Estlander et al., 2017; Lebret et al., 2018). Individuals were not measured if they were damaged or partly hidden.

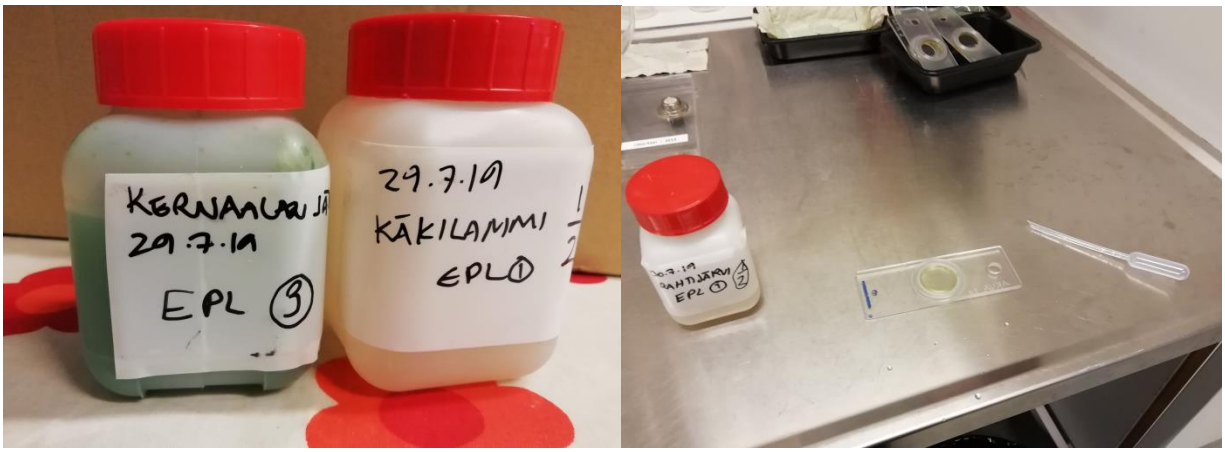


Figure 4. Zooplankton samples were stored in plastic bottles with formaldehyde. Lake Kernaalanjärvi had a cyanobacteria bloom giving it its green colour (left). Small samples amounts were then inserted on top of a glass plate with a pipette for microscoping (right).

Figure 5. Two Daphnia sp. individuals. The measured body length is from upper corner of the eye to the start of the spike. These Daphnia species differ morphologically from each other.

2.2 Organizing the data and statistical analysis

All lakes from both data sets were sorted into groups based on their DOC concentration (Table 1). In DOC group 1 are the lakes with DOC concentrations <10 mg l^{-1}, in the group 2 those with DOC 10-20 mg l^{-1} and in group 3 lakes with DOC concentration >20 mg l^{-1}. In this thesis, I refer to these groups also as low, moderate and high DOC concentrations. The lakes were additionally divided into groups based on the hypothetical DOC threshold of 10-14 mg l^{-1}. Threshold values indicate whether DOC concentrations were under (1), in-between (0) or above (2) the hypothetical threshold. For the SUSFISH samples the average body length of the cladocerans from years 2007-2013 were used for these analyses. Additionally, a weighted average cladoceran body length for each lake was calculated. The statistical analyses were conducted with the statistical software SPSS (IBM Corp. Released 2017. IBM SPSS Statistics for Windows, Version 25.0. Armonk, NY: IBM Corp.)

Table 1. HUMI and SUSFISH lake grouping based on DOC threshold and DOC concentrations.

Number of lakes in data grouping: According to DOC levels			
	Low (DOC_1) <10 mg l^{-1}	Moderate (DOC_2) 10-20 mg l^{-1}	High (DOC_3) >20 mg l^{-1}
HUMI	3	3	3
SUSFISH	2	2	2
Number of lakes in data grouping: According to threshold of 10-14 mg l^{-1}			
	Under threshold (1)	in-between (0)	Above (2)
HUMI	3	1	5
SUSFISH	2	0	4

To study whether the cladoceran community structure changes abruptly once the DOC concentrations exceed a certain threshold (10-14 mg l^{-1}), the variance of cladoceran densities above and below this threshold were analysed using t-tests. T-tests were also used to investigate whether cladoceran body lengths above and below the threshold differ from each other. In case that the homogeneity of variance was violated, the t-test results in which equal variance was not assumed were used for analyses. Cladoceran genera were analysed both separately and together. This same approach was used to study changes in phytoplankton densities.

Additionally, I studied whether these changes in cladocerans densities and body lengths might occur along the DOC gradient. Linear regression was used to quantify the association between environmental factors and the body length of cladocerans. Furthermore, the association between phytoplankton densities to environmental variables was studied accordingly.

To study the variance between the average body length of the cladocerans between the DOC groups (low, moderate and high), the analysis of variance (ANOVA) was used. In those cases, in which the homogeneity of variance was violated, the Brown-Forsythe test was used. Moreover, the Games-Howell post-hoc test was used instead of Tuckey's when the homogeneity of variance was violated. The statistical analyses were focused on the HUMI data which were then, to some extent, compared to the SUSFISH data to find common trends.

Linear regression was used to analyze the relationship between DOC concentration and water colour, thermocline depth, total phosphorus (TP) and chlorophyll a from the HUMI data (Appendix 1). The relationship between DOC and the environmental variables (e.g. light attenuation, suspended solids) were analyzed with Pearson correlation. Additionally, the association between chlorophyll a to phosphorus ratio and DOC concentration was studied with Pearson correlation to determine whether the shading reduces primary production.

3 Results

3.1 Changes in the community structure of zooplankton

Zooplankton were most abundant with DOC concentrations around 20 mg l^{-1} in the studied lakes but the community structure (densities and genera composition) did not change significantly along the DOC gradient, between the three DOC groups nor the DOC threshold groups. However, there were major variation between densities and species composition between the lakes. The abundance of rotifers and copepods was highest in Lake Kyynäröjärvi and Lake Majajärvi (Fig. 6). Rotifers were the most plentiful phylum in all the lakes except in Lake Valkea-Mustajärvi.

DOC concentrations had a significant effect only on *Diaphanosoma* sp. densities, but no effect on other cladoceran genera was observed. DOC concentration explained 53 % of the density increase in the rather large cladoceran genus *Diaphanosoma* sp. in the HUMI samples (Regression: $R^2 = 0.53$, $F_{1,6} = 6.70$, $p < 0.05$). Cladocerans were the most numerous in Lake Majajärvi (>1600 individuals ind. l^{-1}) and lowest densities were in Lake Syrjänalunen, Lake Valkea-Mustajärvi and Lake Rahtijärvi (<25 individuals ind. l^{-1}). The cladoceran densities varied between 80-300 individuals ind. l^{-1} in the remaining lakes. The relative proportions of different cladoceran taxa varied greatly between the lakes, but regardless of DOC concentration (Fig. 7).

The number of measured individuals in each genus varied between the DOC groups 1-3 (Appendix 5). *Bosmina* sp. and *Diaphanosoma* sp. were abundant in all the groups (n > 100). *Daphnia* sp. were plentiful in moderate and high DOC concentrations (n > 100), but rare in low DOC concentrations (n < 50). *Ceriodaphnia* sp. were common in low and high DOC concentrations (n > 100), but sparse in moderate DOC concentrations (n < 40).

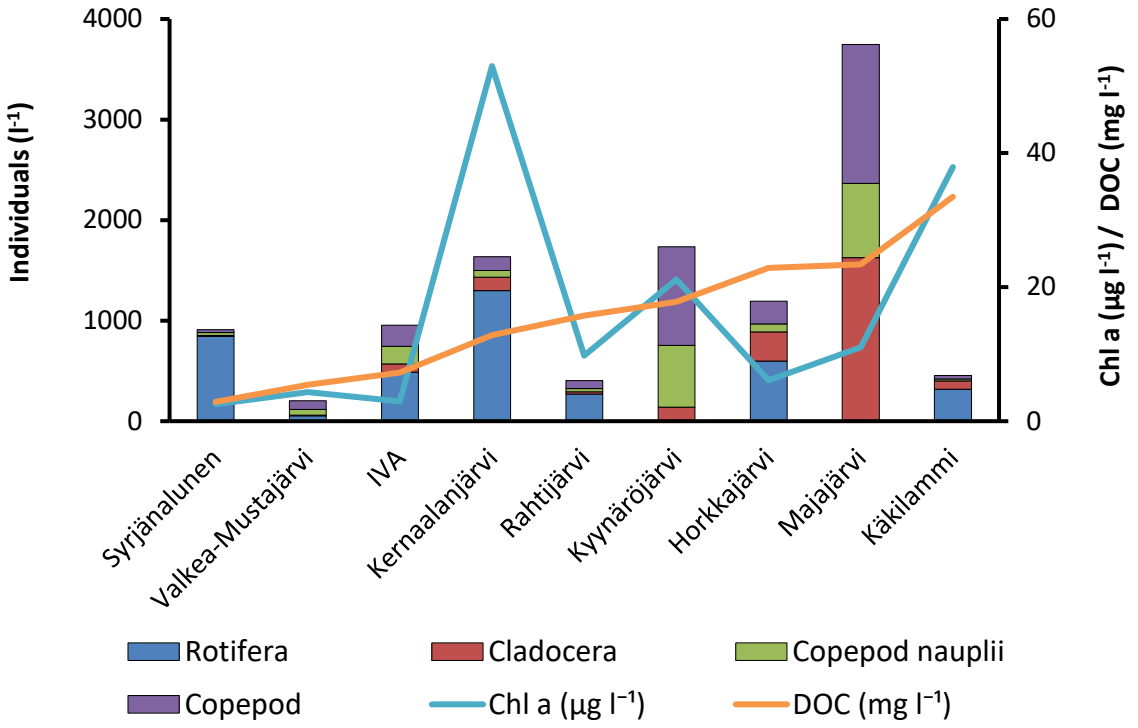


Figure 6. Stacked column of zooplankton densities (individuals ind. l^{-1}) with the DOC and chlorophyll a concentrations in the HUMI lakes. Rotifers for Lake Kyynäröjärvi and Lake Majajärvi are excluded (73% and 66% respectively of total zooplankton density).

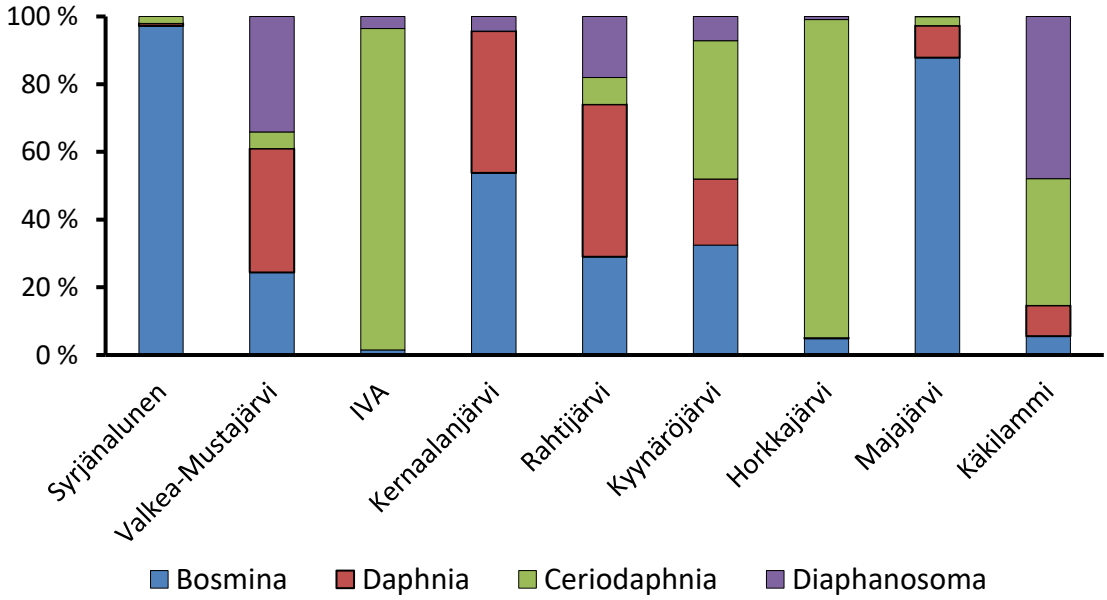


Figure 7. Relative abundance of various cladoceran taxa in the studied lakes. The lakes are arranged so that from left to right the DOC concentration increases.

3.2 Cladoceran body length

There was no significant linear change in weighted average body length of cladocerans along the DOC gradient. Furthermore, the weighted body length showed no significant difference between the three DOC groups (from low to high DOC concentrations). In most lakes, the average cladoceran body length was between 400-450 µm. However, in three lakes the cladoceran body lengths differed notably from the mean values: Lake Syrjänalunen (213 µm), Lake Kyynäröjärvi (345 µm), Lake Majajärvi (321 µm) (Fig. 8).

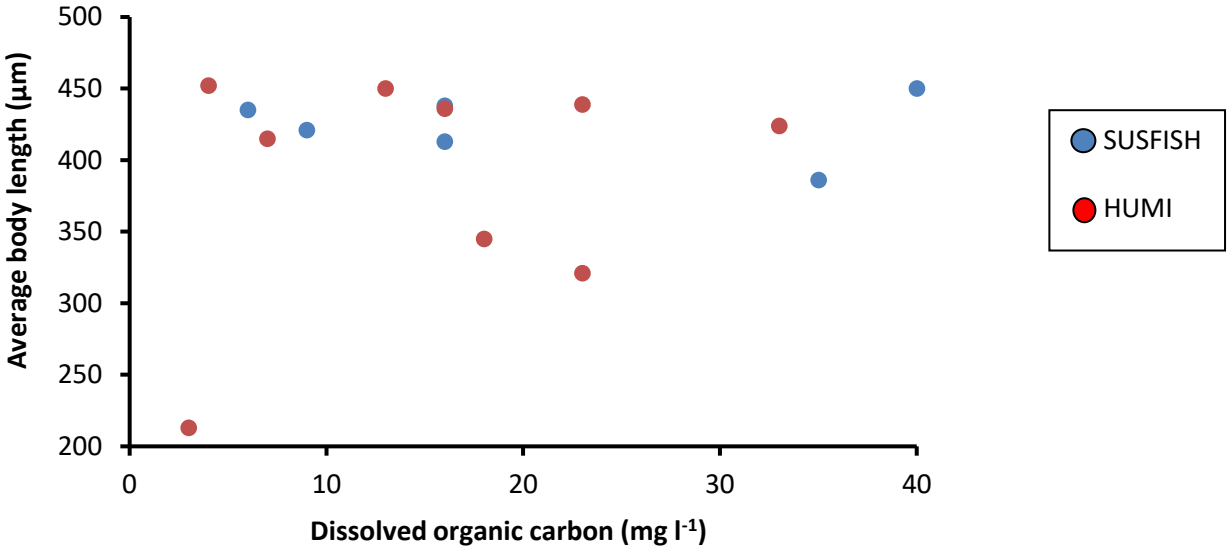


Figure 8. Weighted average body lengths of cladocerans (Bosmina sp., Daphnia sp., Ceriodaphnia sp., Diaphanosoma sp.) plotted against the DOC concentrations.

The cladoceran body length showed a lot of variability between genera and within each genus. The length varied between lakes and between years in the SUSFISH samples. In general, *Bosmina* sp. was the smallest of the four measured genera followed by *Ceriodaphnia* sp. (Appendix 2). *Daphnia* sp. and *Diaphanosoma* sp. were the largest of the studied genera but had also the highest variation in length.

Linear regression showed a significant relation between DOC concentrations and *Diaphanosoma* sp. body length in the HUMI samples, explaining 52 % of the decrease in body length (Regression: $R^2 = 0.52$, $F_{1,7} = 7.69$, $p < 0.05$) (Fig. 9). Though, this was not observed in the SUSFISH samples. Chlorophyll

a concentrations explained 58 % of the decrease in body length of *Ceriodaphnia* sp. in the HUMI data (Regression: R^2 = 0.58, $F_{1,6}$ = 8.32, p < 0.05) and 40 % when including the SUSFISH data (Regression: R^2 = 0.40, $F_{1,12}$ = 8.15, p < 0.05).

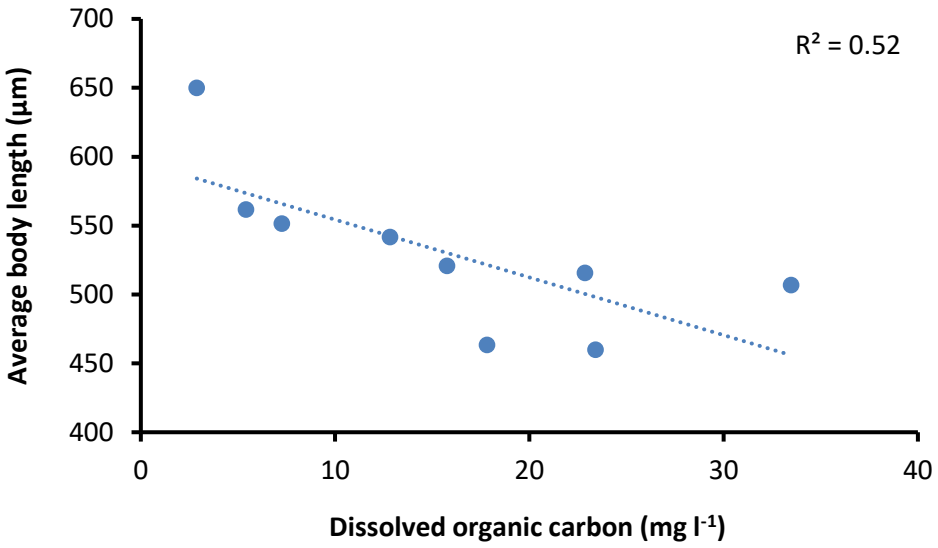


Figure 9. Body length (µm) of Diaphanosoma sp. in the HUMI samples plotted against DOC concentration.

In the HUMI data, the average cladoceran body length was smaller below the DOC threshold of 12 mg l^{-1} (398 µm) than above the threshold (415 µm) (t-test; $t_{623.91}$ = 2.07, p < 0.05). When analysing the body lengths of each genera separately, the body lengths of *Ceriodaphnia* sp. was larger below (407 µm) than above (381 µm) the DOC threshold (t-test; $t_{227.79}$ = -3.35, p < 0.01) (Fig. 10). Also, *Diaphanosoma* sp. was significantly larger below (556 µm) than above (502 µm) the threshold (t-test; $t_{193.71}$ = -5.31, p < 0.01). However, the body length of *Bosmina* sp. was smaller below (248 µm) than above (290 µm) the threshold (t-test; t_{405} = 5.97, p < 0.01). *Daphnia* sp. showed no significant change in body length regarding the DOC threshold.

Similarly to the HUMI data, the *Ceriodaphnia* sp. from the SUSFISH data were larger below (441 µm) than above (410 µm) the threshold (t-test; $t_{978.89}$ = -6.58, p < 0.01) (Fig. 10). Also, *Diaphanosoma* sp. were larger below (697 µm) than above (657 µm) the threshold (t-test; t_{305} = -2.33, p < 0.05). Opposite to the Humi data, the *Bosmina* sp. in the SUSFISH data were larger below (351 µm) than above (324 µm) the threshold (t-test; $t_{1046.17}$ = -8.44, p < 0.01) and *Daphnia* sp. were smaller below (573 µm) than above (656 µm) the threshold (t-test; $t_{831.99}$ = 11.49, p < 0.01).

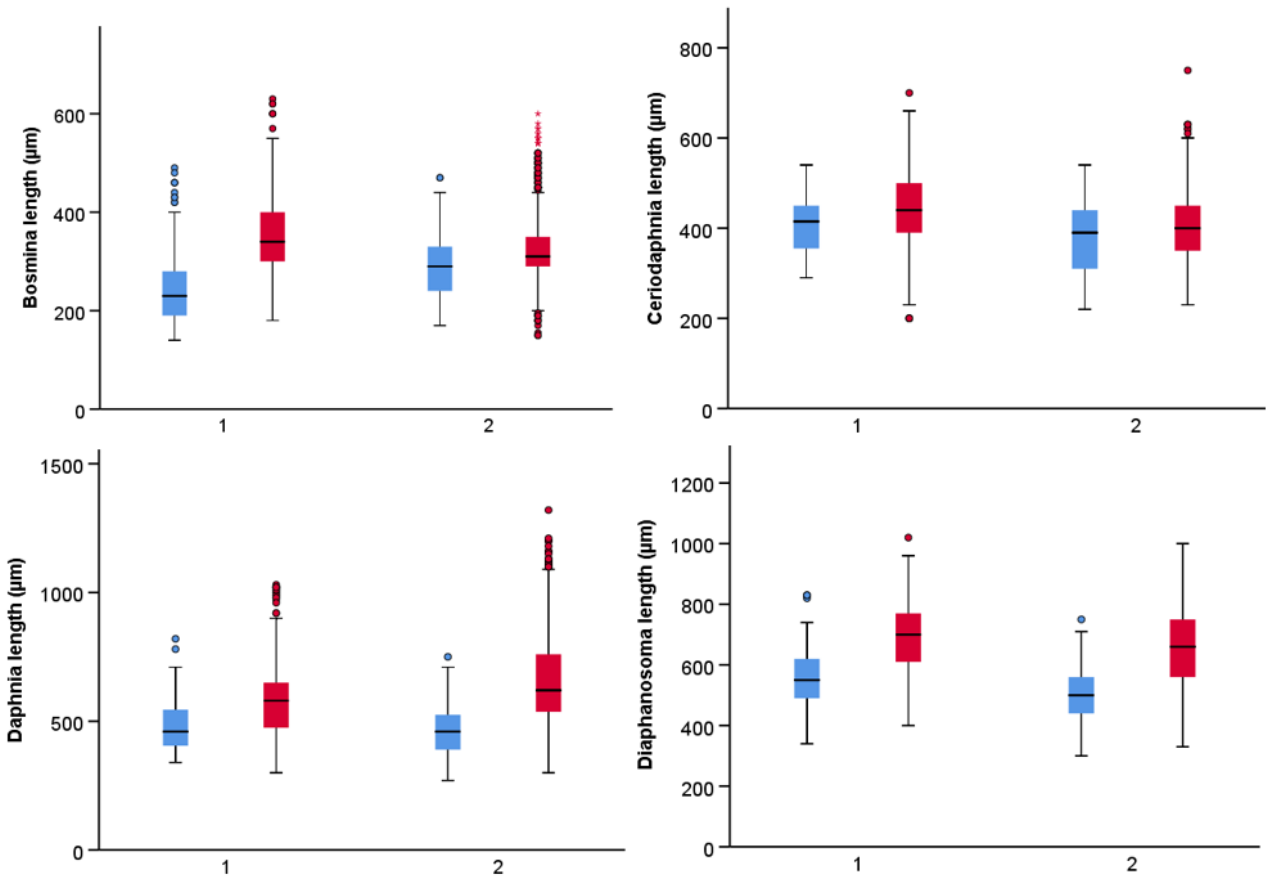


Figure 10. Average body length (µm) of the studied cladoceran genera (Bosmina sp., Ceriodaphnia sp., Daphnia sp., Diaphanosoma sp.) below the threshold (1) and above the threshold (2). Humi data = blue, SUSFISH data = red.

Interestingly, all studied cladoceran genera were on average larger in the SUSFISH data compared to the HUMI data. *Bosmina* sp. in the HUMI data were 276 µm and in the SUSFISH data 330 µm (t-test; $t_{546.61} = 14.52$, $p < 0.01$). *Ceriodaphnia* sp. in the HUMI data were 389 µm and in the SUSFISH data 431 µm (t-test; $t_{605.55} = 9.29$, $p < 0.01$). *Daphnia* sp. in the HUMI data were 496 µm and in the SUSFISH data 641 µm (t-test; $t_{640.83} = 20.64$, $p < 0.01$) and *Diaphanosoma* sp. in the HUMI data were 519 µm and in the SUSFISH data 657 µm (t-test; $t_{636.01} = 16.90$, $p < 0.01$).

In the DOC groups, the average cladoceran body length was smallest (398 µm) in low, largest in moderate (441 µm) and in-between in high DOC concentrations (415 µm) (Brown-Forsythe: $F_{2,1314.24} = 12.34$, $p < 0.01$). The DOC concentration affected significantly on cladoceran body length in all genera for both, HUMI and SUSFISH data sets (Table 2). *Bosmina* sp. were the largest in high DOC concentrations, *Daphnia* sp. in moderate, *Ceriodaphnia* sp. and *Diaphanosoma* sp. in low DOC concentrations (Fig.10). Post hoc test revealed that for all genera in both data sets, except for HUMI

Daphnia sp. samples, the body length between low and moderate DOC groups were significantly different from each other (Appendix 4).

Table 2. Statistical variance analyses of the body length of Bosmina sp., Daphnia sp., Ceriodaphnia sp. and Diaphanosoma sp. between the DOC groups. Test 1 = ANOVA, 2 = Brown Forsythe.

Data	Genus	Test	Homogeneity of variance	df	df2	*F*	*p*
HUMI	*Bosmina sp.*	1	**> 0.05**	2	429	35.38	**< 0.01**
	Daphnia	2	**< 0.01**	2	172.82	10.82	**< 0.01**
	Ceriodaphnia sp.	2	**< 0.05**	2	102.38	5.12	**< 0.01**
	Diaphanosoma sp.	1	**> 0.05**	2	409	16.67	**< 0.01**
SUSFISH	*Bosmina sp.*	2	**< 0.01**	2	1617.33	110.43	**< 0.01**
	Daphnia	2	**< 0.01**	2	1279.32	78.39	**< 0.01**
	Ceriodaphnia sp.	2	**< 0.01**	2	254.28	24.28	**< 0.01**
	Diaphanosoma sp.	1	**> 0.05**	2	363	5.18	**< 0.01**

Concerning the DOC grouping of the HUMI data, the average body length of *Bosmina* sp. seemed to increase towards the higher DOC concentrations (groups 2 and 3) (Fig. 11). The average body length of *Ceriodaphnia* sp. decreased in the higher DOC concentrations. *Daphnia* sp. body length was largest in moderate DOC concentrations (group 2) and smaller in low (group 1) and high DOC concentrations (group 3). *Diaphanosoma* sp. was largest in low DOC concentrations (group 1), decreasing in moderate (group 2) and increasing again in high DOC concentrations (group 3). There was strong variation in the body lengths of *Bosmina* sp. and *Daphnia* sp. in the low and moderate DOC concentrations. For *Diaphanosoma* sp. the only outliers were found in low DOC concentrations.

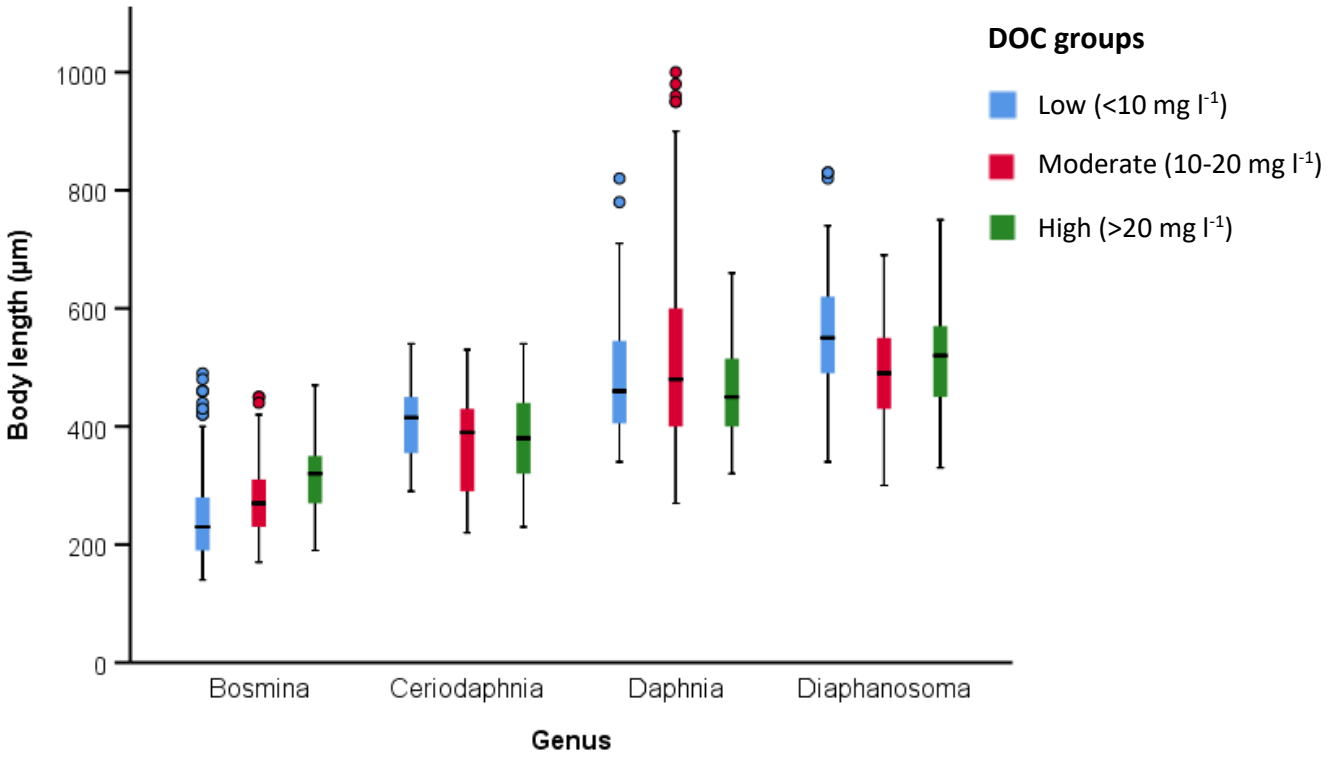


Figure 11. Boxplot of cladoceran genera body length (µm) in each DOC group from the HUMI data.

3.3 Impacts on phytoplankton communities

Similar to the zooplankton communities, the phytoplankton abundance and composition did not change significantly along the DOC gradient, between the DOC groups nor the DOC threshold, but they varied between the lakes (Fig. 12). The total algal abundance (cell l^{-1}) was highest in Lake Kernaalanjärvi (>21M cells l^{-1}) followed by Lake Kyynäröjärvi (>7M cells l^{-1}), where cyanobacterial blooms were also detected. Phytoplankton densities in Lake Iso Valkjärvi, Rahtijärvi and Käkilammi were roughly on the same level (1.5-2M cells l^{-1}). Syrjänalunen, Valkea-Mustajärvi, Horkkajärvi and Majajärvi had the least phytoplankton (<0.75M cells l^{-1}).

In Lake Kernaalanjärvi, the most abundant algae based on cell l^{-1} were the cyanobacteria, also known as blue green algae. In Lake Rahtijärvi and Lake Kyynäröjärvi the most common group were the *Bacillariophyceae* and in all the other lakes, the community structure was more diverse and evenly distributed. Common algae groups that were present in all the lakes were *Chlorophyta*, *Chrysophyceae* and *Cryptophyceae*.

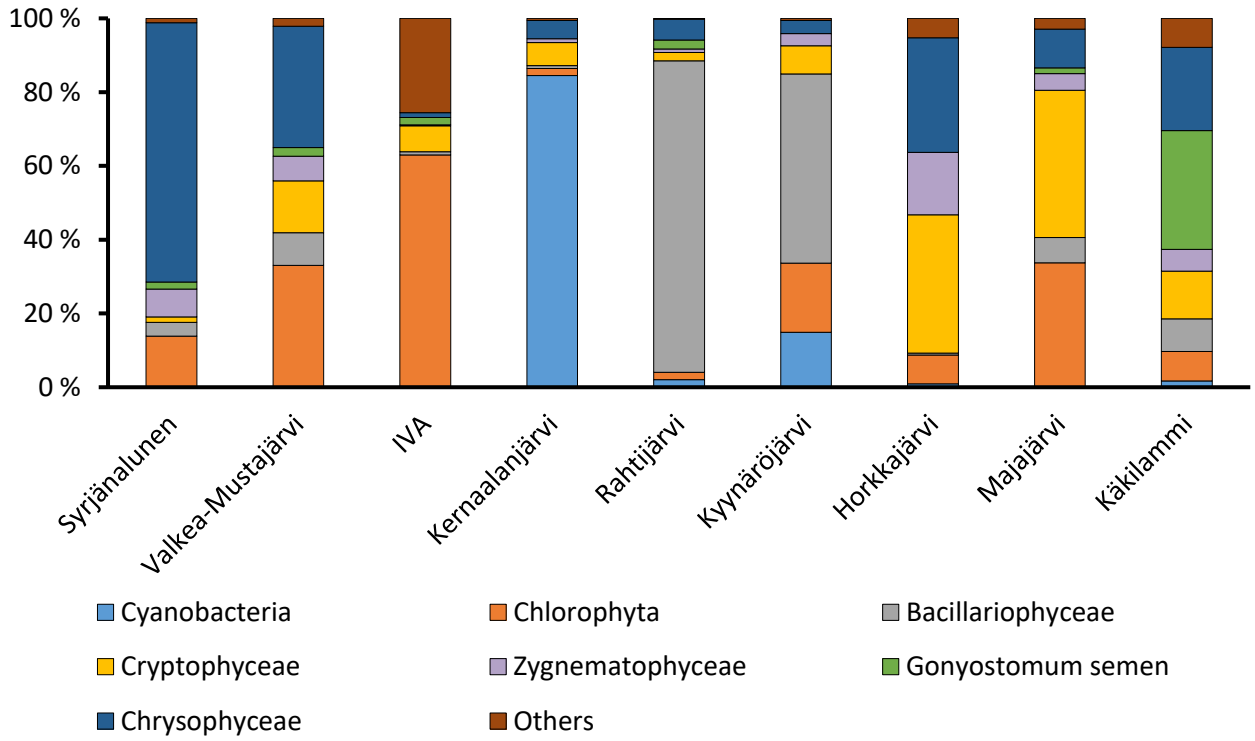


Figure 12. Relative abundance of algae groups in the studied lakes. The lakes are arranged so that from left to right the DOC concentration increases.

3.4 DOC and other environmental variables

DOC concentrations in the studied lakes varied between 2.4-33.5 mg l^{-1} (Appendix 1). There was a strong positive linear relationship between DOC and water colour, and DOC concentrations explained 95% of the water colour variation (Regression: $R^2 = 0.95$, $F_{1,48} = 897.29$, $p < 0.01$) (Fig. 13). DOC had a significant negative effect on thermocline depth concentration and it explained 53 % of the variation in thermocline depth (Regression: $R^2 = 0.53$, $F_{1,38} = 42.28$, $p < 0.01$) (Fig. 14).

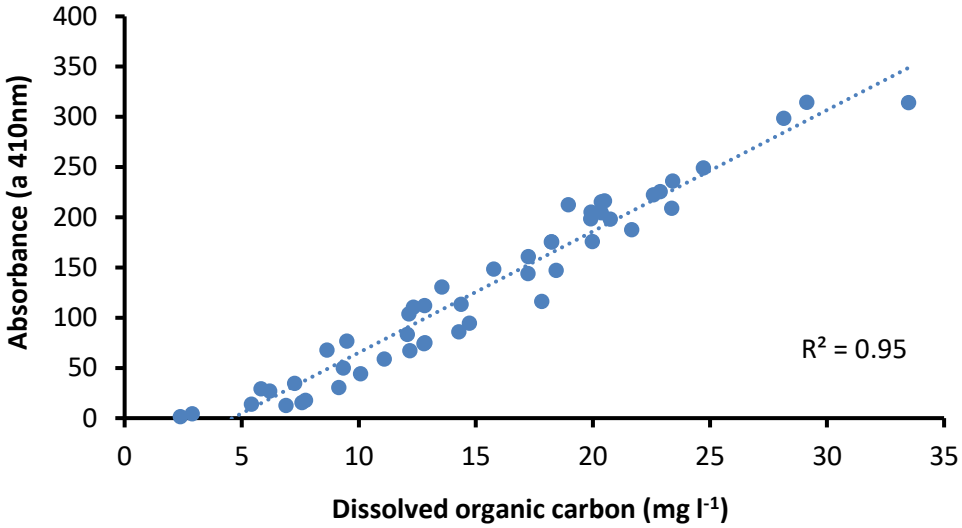


Figure 13. Correlation between DOC concentration and water colour (absorbance a 410 nm)

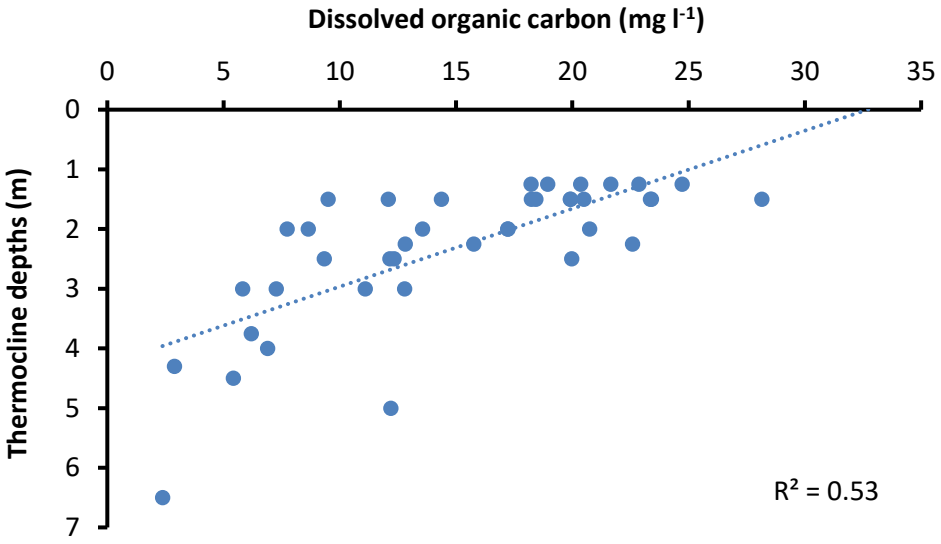


Figure 14. Correlation between DOC concentration and thermocline depth.

The relationship between DOC and chlorophyll a suggested a sudden increase in chlorophyll a levels as DOC concentrations were around 12 mg l^{-1} (Regression: $R^2 = 0.21$, $F_{1,48} = 12.64$, $p < 0.01$) (Fig. 15). Below this threshold value, the chlorophyll a concentrations were around 5 µg l^{-1}. Lake Hosiolammi was an exception, because the chlorophyll a was 18.4 µg $l^{-1}$and DOC only 7.7 mg l^{-1}. However, this lake was eutrophic and had TP values of 28 µg l^{-1}. There were also lakes, which had low chlorophyll a levels despite moderate to high DOC concentrations.

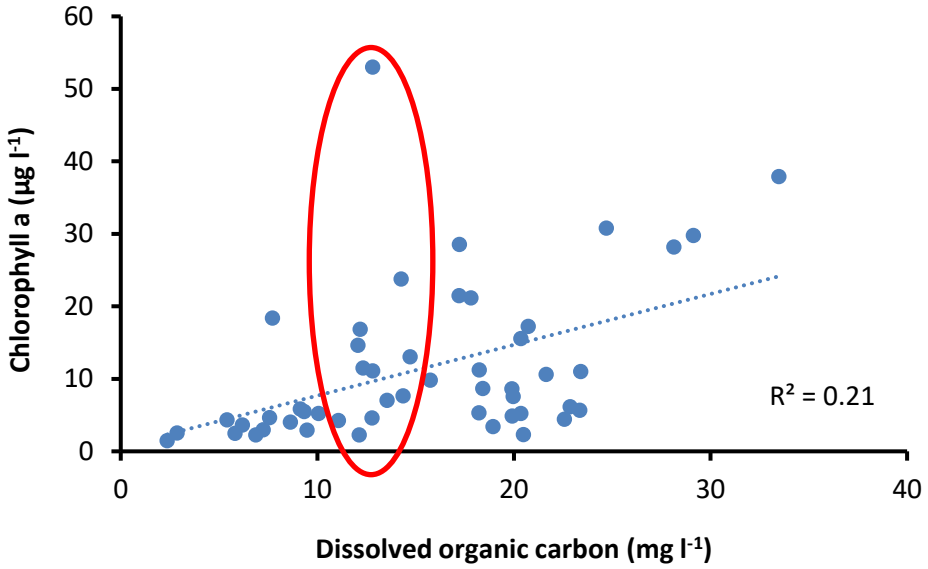


Figure 15. Relationship between DOC concentration and chlorophyll a from the HUMI data set.

Also, TP values increased as DOC concentrations increased (Regression: $R^2 = 0.26$, $F_{1,48} = 16.78$, $p < 0.01$) (Appendix 1). The highest TP values of > 60 µg l^{-1} which were found in Lake Kernaalanjärvi and Lake Kyynäröjärvi had moderate DOC concentrations of 12,8 mg l^{-1} and 17,8 mg l^{-1}, respectively. Most of the studied lakes had TP values below 20 µg l^{-1} and chlorophyll a values below 10 µg l^{-1}. Higher chlorophyll a concentrations were more common once the TP concentrations exceeded 20 µg l^{-1}. The chlorophyll a to phosphorus ratio increased slightly as DOC concentration increased (Fig. 16). There were few high chlorophyll a to TP ratio values at DOC 12 mg l^{-1} as well as between 25-30 mg l^{-1} and multiple low values between DOC concentrations 15-25 mg l^{-1}.

The data showed a strong relationship between DOC and multiple environmental factors (Table 3). DOC correlated at the $p < 0.01$ significance level with TN, COD and light extinction factor (Ɛ). Significant correlation at the $p < 0.05$ level was found between DOC and chlorophyll a to TP ratios. The data showed no significant correlation between DOC and suspended solids or turbidity.

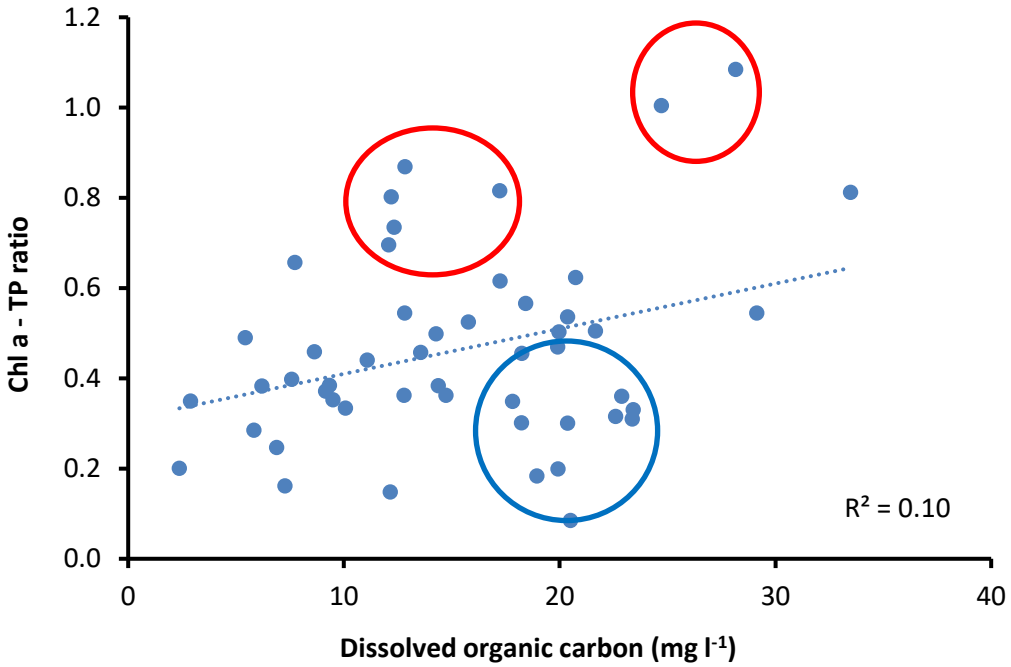


Figure 16. Relationship between DOC concentration and chlorophyll a to total phosphorus ratio.

Table 3. Correlations between DOC and multiple environmental variables. Turb NTU = turbidity, Chl a = chlorophyll a, TN = total nitrogen, COD = chemical oxygen demand, Chl/TP = chlorophyll to phosphorus ratio.

Variables	Pearson Correlation	p	N
Light attenuation (Ɛ)	0.67	**< 0.01**	50
Susp. solids (mg l^{-1})	0.17	0.23	50
Turb NTU (0-1 m)	0.01	0.93	50
Chl a (µg l^{-1})	0.46	**< 0.01**	50
TN (µg l^{-1})	0.66	**< 0.01**	50
COD (mg l^{-1})	0.99	**< 0.01**	50
Chl/TP	0.32	**< 0.05**	50

4 Discussion

The hypotheses of this thesis were that the body length and community structure of the cladocerans would abruptly change once the DOC concentration exceeded the threshold (10-14 mg l^{-1}). This hypothesis was strengthened by the observation that chlorophyll a levels increased abruptly at DOC concentrations of roughly 12 mg l^{-1}. Using the trophic cascade theory, the increase of chlorophyll a could have been caused by the reduced phytoplankton filtration rates from smaller cladoceran densities or individuals body sizes. The results of this study did not support the hypothesis of a sudden change in cladoceran communities at the DOC threshold. The observed sudden peak in the chlorophyll a concentration was likely not solely due to changes in cladoceran densities or their body length. Cladoceran body length changes were also not homogeneous and changes varied between genera. In the Humi data, in high DOC concentrations *Ceriodaphnia* sp. and *Diaphanosoma* sp. were smaller, *Bosmina* sp. were larger and *Daphnia* sp. changes showed no clear trend. The data also showed, that average body length of cladocerans was a little smaller below compared to above the DOC threshold.

Phytoplankton communities varied between the studied lakes, but no clear trends dependent on DOC concentration were observed. Eutrophic lakes e.g. Lake Kernaalanjärvi was dominated by cyanobacteria, which is typical for nutrient rich lakes during summer (Wetzel, 2001). It was also hypothesized that the chlorophyll a to phosphorus ratio would decrease while the DOC concentration increased. This hypothesis was not confirmed as the ratio was increasing in higher DOC concentrations. However, there were multiple low ratio values at higher DOC concentrations (15-25 mg l^{-1}) which could indicate the shading impacts of DOC.

4.1 Factors affecting cladoceran length

In general, the changes in cladoceran size and community structure are caused by environmental and biological factors (Hart & Bychek, 2011). The average cladoceran length stayed surprisingly leveled except for Lake Syrjänalunen, Lake Kyynäröjärvi and Lake Majajärvi (Fig. 8). It could be hypothesized that Lake Syrjänalunen is a clear lake, thus the larger cladocerans might have been hiding in the deeper water layers during daytime when samples were taken (Wetzel, 2001). This

would explain the low average body length even though larger individuals were expected due to the low nutrient levels and competitive advantages of large individuals (Brooks & Dodson, 1965). However, opposite results that small individuals outcompete large individuals in low nutrient levels are also possible (Romanovsky & Feniova, 1985). Such variation in body length, especially if it is due to water colour, makes it fair to criticize whether it is reliable to compare densities and communities between lakes from which the samples have been taken at similar depths. Both Lake Kyynäröjärvi and Lake Majajärvi that had low cladoceran average body lengths, had the highest abundance of zooplankton including rotifers, cladocerans and copepods. This indicates towards a density-controlled impact on the body length of cladocerans.

The HUMI and SUSFISH results on cladoceran body length differed to some extent. All studied genera were larger in the SUSFISH samples. The reasons remain unclear, but HUMI samples consisted of a single sampling time and yearly variation or cladoceran succession are likely to affect the results. Controversially to the SUSFISH data, the *Bosmina* sp. in the HUMI data were smaller below the DOC threshold. Observed similarities between the samples were that the average body lengths of *Ceriodaphnia* sp. and *Diaphanosoma* sp. were smaller above the threshold of 12 mg l^{-1} and similar results were observed in the DOC groups analyses as well. The smaller body sizes at higher DOC concentrations could be linked to the increased food availability and reduced importance of body size in the inter- and intraspecies competition resulting in smaller individuals (Brooks & Dodson, 1965; Gliwicz, 1990).

High predation by fishes can have a significant impact on cladoceran body length potentially driving cladoceran communities towards smaller species and individuals (Korosi et al., 2013; Nevalainen & Luoto, 2013). The HUMI and SUSFISH data did show a general decrease in the body length in the genera *Ceriodaphnia* sp. and *Diaphanosoma* sp. towards higher DOC concentrations. However, the average cladoceran body length was larger above the DOC threshold which could indicate the increased invertebrate predation at higher DOC concentrations (Liljendahl-Nurminen et al., 2008). The role of predation remains unclear due to the absence of predatory data in the HUMI data.

Aside from these factors, there are multiple others that I have not yet addressed in this thesis. A major component affecting pre-determined species body sizes are genes. Cladocerans in this study were only identified to genus level. Naturally, some species within a family are bigger than others and there are major size and morphological differences between species within a genus e.g. *Daphnia*

pulex and *Daphnia magna* (Smith & Cooper, 1982). Some *Daphnia* sp. species like *Daphnia cucullata* also go through cyclomorphosis changing their morphology drastically within a year. Cladocerans have a life cycle from couple of months to even 14 months (Pietrzak et al., 2013). Younger individuals usually tend to be smaller than adult individuals. This study did however not estimate the impact of age on the length distribution of the genera. It is possible, that the seasonal development of cladocerans varied between lakes and large individuals in oligotrophic lakes were also older. Genetic alterations in body length or morphology might also be related to past changes of environmental conditions (Frisch et al., 2014). It remains also to be investigated how parasites might impact cladoceran body length and community structure.

The impacts of DOC on cladoceran body length are challenging to predict, because there are so many impacting components. Based on the results, it can be said, that changes in the DOC concentrations are reflected in the average body length of cladocerans in a complex way and that there are differences between genera.

4.2 Community structure of zooplankton

Changes in cladoceran community structure were difficult to interpret. This study did not observe any clear relationship between a DOC concentration threshold and the cladoceran community structure. The results suggest that the cladocerans are more evenly distributed between genera in moderate DOC concentrations (Fig. 7). In two out of three lakes of both low and in high DOC concentrations either *Bosmina* sp. or *Ceriodaphnia* sp. were the most dominant genus.

Zooplankton were more abundant in lakes with moderate or high DOC concentrations and nutrient levels. However, Lake Käkilammi showed low zooplankton abundances despite high nutrient levels and chlorophyll a value. This might be due to unfavourable environmental conditions, food sources or even increased invertebrate predation. Lake Käkilammi was the only lake in which both the predatory cladocerans *Leptodora kindtii* and *Polyphemus sp.* were found. High relative abundance of the rather large cladoceran *Diaphanosoma* sp. in the dark water Lake Käkilammi could be from the reduced predation pressure from fishes and invertebrate predators that prefer smaller size cladocerans (Liu et al., 2009; Korosi et al., 2013).

The HUMI data does not include any information on predation and fish abundance and therefore no statements can be statistically proven. The lack of data makes it challenging to explain a phenomenon but not necessarily to observe one. Moreover, I believe that the impact of predation in controlling cladocerans densities weakens at higher DOC concentrations. Firstly, the predation conditions for fish worsen (lower light and oxygen concentrations) and secondly, the fish and invertebrates might not be able to control the cladoceran abundance when nutrient levels are high enough (Smith & Cooper, 1982; Utne, 1997). In the HUMI data, copepods were more abundant in lakes with high cladoceran densities and cladocerans were larger above the DOC threshold. Therefore, I also suspect a shift in the predator communities towards a more invertebrate dominated community upon rising DOC concentrations (Liljendahl-Nurminen et al., 2008).

4.3 Impacts of DOC on the lake ecosystem and phytoplankton abundance

The observed results on the effects of dissolved organic carbon in the lake were in accordance to the literature (Solomon et al., 2015). As DOC concentration increased, the lake became more coloured, thermocline depth decreased, nutrient levels rose, and COD increased.

The shading impacts of DOC on primary production was only partly observed in the chlorophyll a to phosphorus ratio values in moderate to high DOC concentrations (15-25 mg l^{-1}) (Fig. 15). It might be that coloured lakes do not produce less chlorophyll a per unit of TP than clear lakes, but additionally to DOC, it is also related to suspended solids, lake circulation and measuring methods (Havens & Nürnberg, 2004). Moreover, the data only contains information on total phosphorus. Not all phosphorus is biologically available and only phosphate in the forms of H_2PO_4–, HPO_4^{2}–, PO_4^{3-} are directly usable by phytoplankton (Boström et al., 1988). Humic substances can bind phosphorus and thus potentially reducing the availability of this nutrient. Chlorophyll a concentration and the ratio values can thus not be entirely explained with only TP concentrations.

Both, Lake Kernaalanjärvi and Lake Kyynäröjärvi had high nutrient levels but only moderate DOC concentrations. Even though Lake Käkilammi has similar nutrient levels as the two previous lakes, the chlorophyll a and phytoplankton abundance were smaller, indicating a shading impact of DOC. It seems that at high DOC concentrations the shading impacts would limit primary production. The results indicate that the phytoplankton biomasses are regulated by DOC concentration which affect

both positively via nutrients and negatively via light extinction (Bergström & Karlsson, 2019). The phytoplankton community structure seemed to be more monotonous at moderate DOC concentrations and diverse in low and high DOC concentrations. The communities varied greatly, however, no clear trends towards DOC concentrations was observed.

4.4 Challenges with the data and uncertainties

There were many challenges concerning the data. The DOC concentrations for the SUSFISH samples were calculated using the water colour values which were collected during October and November while the zooplankton data was from July and August. To test the validity of the equation with which the DOC for the SUSFISH data was calculated, the DOC values were calculated for the HUMI samples as well and compared to measured values. Especially, in DOC concentration below 15 mg l^{-1} the calculated value differed somewhat from the measured one.

The HUMI data consisted of observations from one summer whereas the SUSFISH data contained the average values from multiple years. The yearly variation in measured biological and environmental variables can be immense and therefore caution is necessary when making general statements. For example, cladoceran densities in Lake Majajärvi from the SUSFISH data were roughly 40 individuals ind. l^{-1} and from the same lake in the HUMI data over 1600 individuals ind. l^{-1}. Zooplankton commonly form swarms and density estimates can thus vary greatly depending on the sampling.

This study focused only on four more common genera instead of all cladoceran genera, because their densities remained too little to get any reliable statistical results. Additionally, in Lake Kernaalanjärvi was a Bosminid species (*Bosmina coregoni, Baird, 1857)*, which differed from its morphology compared to other Bosminid species found in the other lakes. Finding *Bosmina coregoni* in Lake Kernaalanjärvi is of no surprise as it is a common species during summer in eutrophic lakes such as the Loosdrecht lakes (Irvine, 1986). In this study, the *Bosmina coregoni* were included in the density analyses, but not in the body length analyses.

4.5 Looking into the future

Looking ahead it could be interesting to conduct a similar study but change the approach a bit. Depending on the exact topic it would be logical to focus on lakes with varying DOC concentrations but similar morphologies and nutrient levels. Additionally, it might be worth considering whether to study a single genus, multiple genera or even just single species. When taking zooplankton samples from lakes with varying DOC concentrations it might be reasonable to assess whether sampling time and depths should be included and to what extent. If the research is more focused on predation, then it might be of benefit to measure additionally to predator densities and cladoceran body length, other body parts such as antennule and mucrone length (Sakamoto & Hanazato, 2008).

It could also be interesting to study whether the impacts of browning are similar across spatially different areas depending on the flexibility of cladoceran communities to adapt to these changes. Clear and pristine lakes might be more sensitive to browning, whereas Finnish lakes that are naturally often humus rich and oligotrophic might handle such changes better.

5 Conclusions

This study showed that DOC concentration has a key role in the lake ecosystem as it impacts many elements such as water colour, thermocline depths and nutrient levels which directly and indirectly affect the cladoceran community structure. Based on the results, the average of body length of cladocerans was larger above the DOC threshold of 12 mg l^{-1}. However, changes in cladoceran body lengths at varying DOC concentration were not monotonous and differed between the studied genera. Both HUMI and SUSFISH data showed a decrease in *Ceriodaphnia* sp. and *Diaphanosoma* sp. body lengths in high DOC concentrations compared to low concentrations. This knowledge could potentially be used when assessing indicators to estimate changes in DOC concentrations. However, cladoceran body length is not unambiguous and a single environmental factor rarely suffices to interpret these changes.

DOC concentrations were poor predictors of cladoceran communities, but cladocerans densities seemed to benefit from elevated DOC concentration due to the increased food availability. The immense variation of environmental variables amidst the lakes makes it challenging to compare these and to give any certain statements. Further studies are needed to understand the complex interactions that happen in cladocerans and food webs as the DOC concentration in northern lakes increase alongside climate change.

6 Acknowledgements

I would like to express my deepest gratitude to my supervisors Dr. Satu Estlander and Prof. Jukka Horppila for the support and advice they gave throughout this Master's Thesis. I am sincerely grateful to Satu for guiding me and helping me overcome various hurdles. I also want to thank Prof. Sakari Kuikka who taught me important things during earlier stages of my Master's studies. I give a big thanks and appreciation to the funding I got from the Maa- ja Vesitekniikan tuki ry. Last but not least, I wish to thank my family, friends and girlfriend for their everlasting support.

7 References

Attayde, J. L., & Ripa, J. (2008). The coupling between grazing and detritus food chains and the strength of trophic cascades across a gradient of nutrient enrichment. *Ecosystems*, *11*(6), 980–990.

Becker, C., Feuchtmayr, H., Brepohl, D., Santer, B., & Boersma, M. (2004). Differential impacts of copepods and cladocerans on lake seston, and resulting effects on zooplankton growth. *Hydrobiologia*, *526*(1 SPEC. ISS.), 197–207.

Berggren, M., Ström, L., Laudon, H., Karlsson, J., Jonsson, A., Giesler, R., Bergström, A. K., & Jansson, M. (2010). Lake secondary production fueled by rapid transfer of low molecular weight organic carbon from terrestrial sources to aquatic consumers. *Ecology Letters*, *13*(7), 870–880.

Bergström, A. K., & Karlsson, J. (2019). Light and nutrient control phytoplankton biomass responses to global change in northern lakes. *Global Change Biology*, *25*(6), 2021–2029.

Bolan, N. S., Adriano, D. C., Kunhikrishnan, A., James, T., McDowell, R., & Senesi, N. (2011). Dissolved Organic Matter. In *Advances in Agronomy* (Vol. 110, Issue C, pp. 1–75).

Boström, B., Persson, G., & Broberg, B. (1988). Bioavailability of Different Phosphorus Forms in Freshwater Systems. In *Phosphorus in Freshwater Ecosystems* (pp. 133–155). Springer Netherlands.

Bowszys, M., Dunalska, J. A., & Jaworska, B. (2014). Zooplankton response to organic carbon level in lakes of differing trophic states. *Knowledge and Management of Aquatic Ecosystems*, *412*.

Brooks, J. L., & Dodson, S. I. (1965). Predation , Body Size , and Composition of Plankton The effect of a marine planktivore on lake plankton. *Science*, *150*(3692), 28–35.

Brown, M. E., Curtin, T. M., Gallagher, C. J., & Halfman, J. D. (2012). Historic nutrient loading and recent species invasions caused shifts in water quality and zooplankton demography in two Finger Lakes (New York, USA). *Journal of Paleolimnology*, *48*(3), 623–639.

Burns, C. W. (1969). Relation between filtering rate, temperature, and body size in four species of Daphnia sp.. *Limnology and Oceanography*, *14*(5), 693–700.

Carpenter, S. R., Cole, J. J., Kitchell, J. F., & Pace, M. L. (1998). Impact of dissolved organic carbon, phosphorus, and grazing on phytoplankton biomass and production in experimental lakes. *Limnology and Oceanography*, *43*(1), 73–80.

Clark, J. M., Bottrell, S. H., Evans, C. D., Monteith, D. T., Bartlett, R., Rose, R., Newton, R. J., & Chapman, P. J. (2010). The importance of the relationship between scale and process in understanding long-term DOC dynamics. *Science of the Total Environment*, *408*(13), 2768–2775.

Clark, Joanna M., Chapman, P. J., Adamson, J. K., & Lane, S. N. (2005). Influence of drought-induced acidification on the mobility of dissolved organic carbon in peat soils. *Global Change Biology*, *11*(5), 791–809.

Cole, J. J., Prairie, Y. T., Caraco, N. F., McDowell, W. H., Tranvik, L. J., Striegl, R. G., Duarte, C. M., Kortelainen, P., Downing, J. A., Middelburg, J. J., & Melack, J. (2007). Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. *Ecosystems*, *10*(1), 171–184.

Cole, Jonathan J., Carpenter, S. R., Kitchell, J., Pace, M. L., Solomon, C. T., & Weidel, B. (2011). Strong evidence for terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen, and hydrogen. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(5), 1975–1980.

del Giorgio, P. A., & Peters, R. H. (1994). Patterns in planktonic *P:R* ratios in lakes: Influence of lake trophy and dissolved organic carbon. *Limnology and Oceanography*, *39*(4), 772–787.

Ebert, D. (2005). Ecology, Epidemiology and Evolution of Parasitism in. In *Evolution* (Vol. 3, Issue 1).

Erlandsson, M., Buffam, I., Fölster, J., Laudon, H., Temnerud, J., Weyhenmeyer, G. A., & Bishop, K. (2008). Thirty-five years of synchrony in the organic matter concentrations of Swedish rivers explained by variation in flow and sulphate. *Global Change Biology*, *14*(5), 1191–1198.

Estlander, S., Horppila, J., Olin, M., & Nurminen, L. (2017). Should I stay or should I go? The diurnal behaviour of plant-attached zooplankton in lakes with different water transparency. *Journal of Limnology*, *76*(2), 253–260.

Fee, E. J., Hecky, R. E., Kasian, S. E. M., & Cruikshank, D. R. (1996). Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. *Limnology and Oceanography*, *41*(5), 912–920.

Forró, L., Korovchinsky, N. M., Kotov, A. A., & Petrusek, A. (2008). Global diversity of cladocerans (Cladocera; Crustacea) in freshwater. *Hydrobiologia*, *595*(1), 177–184.

Freeman, C., Evans, C. D., Monteith, D. T., Reynolds, B., & Fenner, N. (2001). Export of organic carbon from peat soils. *Nature*, *412*(6849), 785.

Frisch, D., Morton, P. K., Chowdhury, P. R., Culver, B. W., Colbourne, J. K., Weider, L. J., & Jeyasingh, P. D. (2014). A millennial-scale chronicle of evolutionary responses to cultural eutrophication in Daphnia sp.. *Ecology Letters*, *17*(3), 360–368.

Geraldes, A. M., & Boavida, M. J. (2004). What factors affect the pelagic cladocerans of the meso-eutrophic Azibo Reservoir? *Annales de Limnologie*, *40*(2), 101–111.

Gliwicz, Z. M. (1990). Food thresholds and body size in cladocerans. *Nature*, *343*(6259), 638–640.

Grey, J., Jones, R. I., & Sleep, D. (2001). Seasonal changes in the importance of the source of organic matter to the diet of zooplankton in Loch Ness, as indicated by stable isotope analysis. *Limnology and Oceanography*, *46*(3), 505–513.

Guilizzoni, P., Levine, S. N., Manca, M., Marchetto, A., Lami, A., Ambrosetti, W., Brauer, A., Gerli, S., Carrara, E. A., Rolla, A., Guzzella, L., & Vignati, D. A. L. (2012). Ecological effects of multiple stressors on a deep lake (Lago Maggiore, Italy) integrating neo and palaeolimnological approaches. *Journal of Limnology*, *71*(1), 1.

Hansell, D. A., & Carlson, C. A. (2014). Biogeochemistry of Marine Dissolved Organic Matter: Second Edition. In *Biogeochemistry of Marine Dissolved Organic Matter: Second Edition*. Elsevier Inc.

Hanson, P. C., Carpenter, S. R., Cardille, J. A., Coe, M. T., & Winslow, L. A. (2007). Small lakes dominate a random sample of regional lake characteristics. *Freshwater Biology*, *52*(5), 814–822.

Hart, R. C., & Bychek, E. A. (2011). Body size in freshwater planktonic crustaceans: An overview of extrinsic determinants and modifying influences of biotic interactions. *Hydrobiologia*, *668*(1), 61–108.

Havens, K. E., & Nürnberg, G. K. (2004). The phosphorus-chlorophyll relationship in lakes: Potential influences of color and mixing regime. *Lake and Reservoir Management*, *20*(3), 188–196.

Hessen, D. O. (1998). *Food Webs and Carbon Cycling in Humic Lakes* (pp. 285–315). Springer, Berlin, Heidelberg.

Holmroos, H. J., Hietanen, S., Niemistö, J., & Horppila, J. (2012). Sediment resuspension and denitrification affect the nitrogen to phosphorus ratio of shallow lake waters. *Fundamental and Applied Limnology*, *180*(3), 193–205.

Hope, D., Kratz, T. K., & Riera, J. L. (1996). Relationship between and Dissolved Organic Carbon in Northern Wisconsin Lakes. *Journal of Environmental Quality*, *25*(6), 1442–1445.

Hutchinson, G. E. (n.d.). The Paradox of the Plankton. In *The American Naturalist* (Vol. 95, pp. 137–145). The University of Chicago PressThe American Society of Naturalists.

Imberger, J. (2011). *Flux paths in a stratified lake: A review* (pp. 1–17). American Geophysical Union (AGU).

Irvine, K. (1986). As an Explanation of Zooplankton Community Structure. *Hydrobiological Bulletin*, *20*(1/2), 121–134.

Jansson, M., Karlsson, J., & Jonsson, A. (2012). Carbon dioxide supersaturation promotes primary production in lakes. *Ecology Letters*, *15*(6), 527–532.

Jeppesen, E., Nõges, P., Davidson, T. A., Haberman, J., Nõges, T., Blank, K., Lauridsen, T. L., Søndergaard, M., Sayer, C., Laugaste, R., Johansson, L. S., Bjerring, R., & Amsinck, S. L. (2011). Zooplankton as indicators in lakes: A scientific-based plea for including zooplankton in the ecological quality assessment of lakes according to the European Water Framework Directive (WFD). In *Hydrobiologia* (Vol. 676, Issue 1, pp. 279–297).

Jones, R. I. (1992). The influence of humic substances on lacustrine planktonic food chains. In *Dissolved Organic Matter in Lacustrine Ecosystems: Energy Source and System Regulator* (pp. 73–91). Springer Netherlands.

Jones, S. E., Solomon, C. T., & Weidel, B. C. (2014). Subsidy or Subtraction: How Do Terrestrial Inputs Influence Consumer Production in Lakes? *Freshwater Reviews*, *5*(1), 37.

Karlsson, J., Byström, P., Ask, J., Ask, P., Persson, L., & Jansson, M. (2009). Light limitation of nutrient-poor lake ecosystems. *Nature*, *460*(7254), 506–509.

Karlsson, J., Jonsson, A., Meili, M., & Jansson, M. (2003). Control of zooplankton dependence on allochthonous organic carbon in humic and clear-water lakes in northern Sweden. *Limnology and Oceanography*, *48*(1 I), 269–276.

Kelly, P. T., Craig, N., Solomon, C. T., Weidel, B. C., Zwart, J. A., & Jones, S. E. (2016). Experimental whole-lake increase of dissolved organic carbon concentration produces unexpected increase in crustacean zooplankton density. *Global Change Biology*, *22*(8), 2766–2775.

Kelly, P. T., Solomon, C. T., Weidel, B. C., & Jones, S. E. (2014). Terrestrial carbon is a resource, but not a subsidy, for lake zooplankton. *Ecology*, *95*(5), 1236–1242.

Kirk, J. (2011). Light and photosynthesis in aquatic environment-Third Edition. In *University Press, Cambridge*. Cambridge University Press.

Kissman, C. E. H., Williamson, C. E., Rose, K. C., & Saros, J. E. (2017). Nutrients associated with terrestrial dissolved organic matter drive changes in zooplankton:phytoplankton biomass ratios in an alpine lake. *Freshwater Biology*, *62*(1), 40–51.

Kling, G. W. (1988). Comparative transparency, depth of mixing, and stability of stratification in lakes of Cameroon, West Africa1. *Limnology and Oceanography*, *33*(1), 27–40.

Koroleff, F. 1979. Methods for the chemical analysis for seawater. Meri 7: 1–60. [In Finnish.].

Korosi, J. B., Kurek, J., & Smol, J. P. (2013). A review on utilizing Bosmina sp. size structure archived in lake sediments to infer historic shifts in predation regimes. *J. Plankton Res*, *35*(2), 444–460.

Korosi, J. B., Paterson, A. M., Desellas, A. M., & Smol, J. P. (2008). Linking mean body size of pelagic Cladocera to environmental variables in Precambrian Shield lakes: A paleolimnological approach. *Journal of Limnology*, *67*(1), 22–34.

Korosi, J. B., & Smol, J. P. (2011). Distribution of cladoceran assemblages across environmental gradients in Nova Scotia (Canada) lakes. *Hydrobiologia*, *663*(1), 83–99.

Kritzberg, E. S., & Ekström, S. M. (2012). Increasing iron concentrations in surface waters – a factor behind brownification? *Biogeosciences*, *9*(4), 1465–1478.

Laine, M. P. P., Strömmer, R., & Arvola, L. (2014). DOC and CO2-C releases from pristine and drained peat soils in response to water table fluctuations: A mesocosm experiment. *Applied and Environmental Soil Science*, *2014*.

Larsen, S., Andersen, T., & Hessen, D. O. (b) (2011). The pCO2 in boreal lakes: Organic carbon as a universal predictor? *Global Biogeochemical Cycles*, *25*(2).

Larsen, S., Andersen, T., & Hessen, D. O. (a) (2011). Climate change predicted to cause severe increase of organic carbon in lakes. *Global Change Biology*, *17*(2), 1186–1192.

Lebret, K., Langenheder, S., Colinas, N., Östman, Ö., & Lindström, E. S. (2018). Increased water colour affects freshwater plankton communities in a mesocosm study. *Aquatic Microbial Ecology*, *81*(1), 1–17.

Liljendahl-Nurminen, A., Horppila, J., & Lampert, W. (2008). Physiological and visual refuges in a metalimnion: An experimental study of effects of clay turbidity and an oxygen minimum on

fish predation. *Freshwater Biology*, *53*(5), 945–951.

Liljendahl-Nurminen, A., Horppila, J., Malinen, T., Eloranta, P., Vinni, M., Alajärvi, E., & Valtonen, S. (2003). The supremacy of invertebrate predators over fish - Factors behind the unconventional seasonal dynamics of cladocerans in Lake Hiidenvesi. *Archiv Fur Hydrobiologie*, *158*(1), 75–96.

Liu, G., Liu, Z., Li, Y., Chen, F., Gu, B., & Smoak, J. M. (2009). Effects of fish introduction and eutrophication on the cladoceran community in Lake Fuxian, a deep oligotrophic lake in southwest China. *Journal of Paleolimnology*, *42*(3), 427–435.

MacIntyre, S., Sickman, J. O., Goldthwait, S. A., & Kling, G. W. (2006). Physical pathways of nutrient supply in a small, ultraoligotrophic arctic lake during summer stratification. *Limnology and Oceanography*, *51*(2), 1107–1124.

Mapcustomizer.com. (n.d.). Retrieved February 25, 2020, from https://www.mapcustomizer.com/

Matthews, B., & Mazumder, A. (2006). Habitat specialization and the exploitation of allochthonous carbon by zooplankton. *Ecology*, *87*(11), 2800–2812.

Mattsson, T., Kortelainen, P., & Räike, A. (2005). Export of DOM from boreal catchments: Impacts of land use cover and climate. *Biogeochemistry*, *76*(2), 373–394.

McCauley, E., & Kalff, J. (1981). Empirical Relationships Between Phytoplankton and Zooplankton Biomass in Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*(4), 458–463.

McDonald, S., Bishop, A. G., Prenzler, P. D., & Robards, K. (2004). Analytical chemistry of freshwater humic substances. In *Analytica Chimica Acta* (Vol. 527, Issue 2, pp. 105–124). Elsevier.

McDowell, W. H., & Likens, G. E. (1988). Origin, Composition, and Flux of Dissolved Organic Carbon in the Hubbard Brook Valley. *Ecological Monographs*, *58*(3), 177–195.

McQueen, D. J., Post, J. R., & Mills, E. L. (1986). Trophic relationships in freshwater pelagic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, *43*(8), 1571–1581.

Minor, E. C., Swenson, M. M., Mattson, B. M., & Oyler, A. R. (2014). Structural characterization of dissolved organic matter: A review of current techniques for isolation and analysis. In *Environmental Sciences: Processes and Impacts* (Vol. 16, Issue 9, pp. 2064–2079). Royal Society of Chemistry.

Mitrovic, S. M., Westhorpe, D. P., Kobayashi, T., Baldwin, D. S., Ryan, D., & Hitchcock, J. N. (2014). Short-term changes in zooplankton density and community structure in response to different sources of dissolved organic carbon in an unconstrained lowland river: Evidence for food web support. *Journal of Plankton Research*, *36*(6), 1488–1500.

Møller, E. F. (2005). Sloppy feeding in marine copepods: Prey-size-dependent production of dissolved organic carbon. *Journal of Plankton Research*, *27*(1), 27–35.

Molot, L. A., & Dillon, P. J. (1997). Colour - mass balances and colour - dissolved organic carbon relationships in lakes and streams in central Ontario. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(12), 2789–2795.

Monteith, D. T., Stoddard, J. L., Evans, C. D., De Wit, H. A., Forsius, M., Høgåsen, T., Wilander, A., Skjelkvåle, B. L., Jeffries, D. S., Vuorenmaa, J., Keller, B., Kopécek, J., & Vesely, J. (2007). Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature*, *450*(7169), 537–540.

Morris, D. P., Zagarese, H., Williamson, C. E., Balseiro, E. G., Hargreaves, B. R., Modenutti, B., Moeller, R., & Queimalinos, C. (1995). The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnology and Oceanography*, *40*(8), 1381–1391.

Neff, J. C., & Asner, G. P. (2001). Dissolved organic carbon in terrestrial ecosystems: Synthesis and a model. *Ecosystems*, *4*(1), 29–48.

Nevalainen, L., & Luoto, T. P. (2013). Limnological deterioration forces community and phenotypic changes in cladocera: tracking eutrophication of mallusjärvi, a lake in southern Finland. In *Boreal Environment Research* (Vol. 18), 209-222.

Nykänen, M., Malinen, T., Vakkilainen, K., Liukkonen, M., & Kairesalo, T. (2010). Cladoceran community responses to biomanipulation and re-oligotrophication in Lake Vesijärvi, Finland, as inferred from remains in annually laminated sediment. *Freshwater Biology*, *55*(6), 1164–1181.

Pace, M. L., Cole, J. J., Carpenter, S. R., Kitchell, J. F., Hodgson, J. R., Van De Bogert, M. C., Bade, D. L., Kritzberg, E. S., & Bastviken, D. (2004). Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. *Nature*, *427*(6971), 240–243.

Palmer, M. E., Yan, N. D., & Somers, K. M. (2014). Climate change drives coherent trends in physics and oxygen content in North American lakes. *Climatic Change*, *124*(1–2), 285–299.

Peters, R. H., & Downing, J. A. (1984). Empirical analysis of zooplankton filtering and feeding rates. *Limnology and Oceanography*, *29*(4), 763–784.

Pietrzak, B., Bednarska, A., Markowska, M., Rojek, M., Szymanska, E., & Slusarczyk, M. (2013). Behavioural and physiological mechanisms behind extreme longevity in Daphnia sp.. *Hydrobiologia*, *715*(1), 125–134.

Power M. E. (1992). Top-down and bottom-up forces in food webs: do plants have primacy. *Ecology*, *73*(3), 733–746.

Prairie, Y. T. (2008). Carbocentric limnology: Looking back, looking forward. In *Canadian Journal of Fisheries and Aquatic Sciences* (Vol. 65, Issue 3, pp. 543–548).

Read, J. S., & Rose, K. C. (2013). Physical responses of small temperate lakes to variation in dissolved organic carbon concentrations. *Limnology and Oceanography*, *58*(3), 921–931.

Riemann, L., & Azam, F. (2002). Widespread N-acetyl-D-glucosamine uptake among pelagic marine bacteria and its ecological implications. *Applied and Environmental Microbiology*, *68*(11), 5554–5562.

Robidoux, M., del Giorgio, P., & Derry, A. (2015). Effects of humic stress on the zooplankton from clear and DOC-rich lakes. *Freshwater Biology*, *60*(7), 1263–1278.

Romanovsky, Y. E. (1984). Competitive Advantages in Cladoceran Crustaceans. *Int. Revue Ges.*

Hydrobiol., *69*(5), 613–632.

Romanovsky, Y. E., & Feniova, I. Y. (1985). Competition among Cladocera: Effect of Different Levels of Food Supply. *Oikos*, *44*(2), 243.

Roulet, N., & Moore, T. R. (2006). Environmental chemistry: Browning the waters. In *Nature* (Vol. 444, Issue 7117, pp. 283–284). Nature Publishing Group.

Sakamoto, M., & Hanazato, T. (2008). Antennule shape and body size of Bosmina sp.: Key factors determining its vulnerability to predacious copepoda. *Limnology*, *9*(1), 27–34.

Sanclements, M. D., Oelsner, G. P., McKnight, D. M., Stoddard, J. L., & Nelson, S. J. (2012). New insights into the source of decadal increases of dissolved organic matter in acid-sensitive lakes of the Northeastern United States. *Environmental Science and Technology*, *46*(6), 3212–3219.

Shapiro, J. (1990). Biomanipulation: the next phase - making it stable. *Hydrobiologia*, *200–201*(1), 13–27.

Skjelkvåle, B. L., Stoddard, J. L., Jeffries, D. S., Tørseth, K., Høgåsen, T., Bowman, J., Mannio, J., Monteith, D. T., Mosello, R., Rogora, M., Rzychon, D., Vesely, J., Wieting, J., Wilander, A., & Worsztynowicz, A. (2005). Regional scale evidence for improvements in surface water chemistry 1990-2001. *Environmental Pollution*, *137*(1), 165–176.

Smith, D. W., & Cooper, S. D. (1982). Competition among Cladocera. *Ecology*, *63*(4), 1004–1015.

Smith, T. M., & Smith, R. L. (2015). Elements of ecology. San Francisco, CA: Pearson Benjamin Cummings.

Sobek, S., Algesten, G., Bergstrom, A.-K., Jansson, M., & Tranvik, L. J. (2003). The catchment and climate regulation of pCO2 in boreal lakes. *Global Change Biology*, *9*(4), 630–641.

Solomon, C. T., Jones, S. E., Weidel, B. C., Buffam, I., Fork, M. L., Karlsson, J., Larsen, S., Lennon, J. T., Read, J. S., Sadro, S., & Saros, J. E. (2015). Ecosystem Consequences of Changing Inputs of Terrestrial Dissolved Organic Matter to Lakes: Current Knowledge and Future Challenges. *Ecosystems*, *18*(3), 376–389.

Sommer, U., & Stibor, H. (2002). Copepoda - Cladocera - Tunicata: The role of three major mesozooplankton groups in pelagic food webs. *Ecological Research*, *17*(2), 161–174.

Steinberg, C. E. W., Kamara, S., Prokhotskaya, V. Y., Manusadzianas, L., Karasyova, T. A., Timofeyev, M. A., Jie, Z., Paul, A., Meinelt, T., Farjalla, V. F., Matsuo, A. Y. O., Kent Burnison, B., & Menzel, R. (2006). Dissolved humic substances - ecological driving forces from the individual to the ecosystem level? *Freshwater Biology*, *51*(7), 1189–1210.

Sweetman, J. N., & Finney, B. P. (2003). Differential responses of zooplankton populations (Bosmina sp. longirostris) to fish predation and nutrient-loading in an introduced and a natural sockeye salmon nursery lake on Kodiak Island, Alaska, USA. *Journal of Paleolimnology*, *30*(2), 183–193.

Tanentzap, A. J., Kielstra, B. W., Wilkinson, G. M., Berggren, M., Craig, N., Del Giorgio, P. A., Grey, J., Gunn, J. M., Jones, S. E., Karlsson, J., Solomon, C. T., & Pace, M. L. (2017). Terrestrial

support of lake food webs: Synthesis reveals controls over cross-ecosystem resource use. *Science Advances*, *3*(3), 1–11.

Tanentzap, A. J., Szkokan-Emilson, E. J., Kielstra, B. W., Arts, M. T., Yan, N. D., & Gunn, J. M. (2014). Forests fuel fish growth in freshwater deltas. *Nature Communications*, *5*(1), 1–9.

Thurman, E. M. (1985). Introduction. In *Organic Geochemistry of Natural Waters* (pp. 1–4). Springer Netherlands.

Tranvik, L. J., Downing, J. A., Cotner, J. B., Loiselle, S. A., Striegl, R. G., Ballatore, T. J., Dillon, P., Finlay, K., Fortino, K., Knoll, L. B., Kortelainen, P. L., Kutser, T., Larsen, S., Laurion, I., Leech, D. M., McCallister, S. L., McKnight, D. M., Melack, J. M., Overholt, E., … Weyhenmeyer, G. A. (2009). Lakes and reservoirs as regulators of carbon cycling and climate. *Limnology and Oceanography*, *54*(6part2), 2298–2314.

Utne, A. C. W. (1997). The effect of turbidity and illumination on the reaction distance and search time of the marine planktivore Gobiusculus flavescens. *Journal of Fish Biology*, *50*(5), 926–938.

Vanni, M. J. (1987). Effects of nutrients and zooplankton size on the structure of a phytoplankton community. *Ecology*, *68*(3), 624–635.

Wetzel, R.G. (2001). Limnology: Lake and River Ecosystem 3rd ed. Academic Press New York 1006 pp.

Wickland, K. P., Aiken, G. R., Butler, K., Dornblaser, M. M., Spencer, R. G. M., & Striegl, R. G. (2012). Biodegradability of dissolved organic carbon in the Yukon River and its tributaries: Seasonality and importance of inorganic nitrogen. *Global Biogeochemical Cycles*, *26*(3).

Williamson, C. E., Morris, D. P., Pace, M. L., & Olson, O. G. (1999). Dissolved organic carbon and nutrients as regulators of lake ecosystems: Resurrection of a more integrated paradigm. *Limnology and Oceanography*, *44*(3part2), 795–803.

Williamson, C. E., Stemberger, R. S., Morris, D. P., Frost, T. M., & Paulsen, S. G. (1996). Ultraviolet radiation in North American lakes: Attenuation estimates from DOC measurements and implications for plankton communities. *Limnology and Oceanography*, *41*(5), 1024–1034.

Wissel, B., & Ramacharan, C. W. (2003). Plasticity of vertical distribution of crustacean zooplankton in lakes with varying levels of water colour. *Journal of Plankton Research*, *25*(9), 1047–1057.

Appendix 1. HUMI data set. Environmental data from 50 study lakes. Zooplankton samples from the bolded lakes.

Lake	DOC mg/l	Secchi (cm)	thermocline (m)	pH (0-1m)	Turb NTU	suspendid s	absorbance	Chl A µg/l	DOC mg/l	CODMn m	Fe mg/l	Tot-N µg l-1	Tot-P µg l-	SpCond uS	Temperatı	E	secchi/absc	Chl/TP
Akkijärvi	12,2	165,0	5,0	6,6	2,3	1,7	67,0	16,8	12,2	12,6	0,7	520,0	21,0	91,4	19,8	3,6	2,5	0,8
Alempi Rajajärvi	18,2	70,0	1,3	5,3	1,4	1,8	175,5	5,3	18,2	21,2	0,5	540,0	17,7	58,8	23,0	5,0	0,4	0,3
Alinen Rautjärvi	12,1	130,0	2,5	6,3	1,8	2,2	103,8	2,3	12,1	13,8	0,5	443,3	15,3	78,8	21,8	2,9	1,3	0,1
Anttilanjärvi	17,2	85,0	2,0	6,7	0,9	3,2	143,8	21,5	17,2	20,2	0,3	643,3	26,3	69,4	22,6	7,6	0,6	0,8
Halsjärvi	9,5	140,0	1,5	6,1	1,3	1,3	76,5	2,9	9,5	11,3	0,5	340,0	8,3	81,0	21,8	3,3	1,8	0,4
Haukijärvi	19,9	65,0	1,5	6,0	6,8	3,6	198,3	8,6	19,9	25,9	1,3	550,0	18,3	82,0	23,0	6,0	0,3	0,5
Haukilammi	20,5	70,0	1,5	5,9	0,9	1,2	216,4	2,3	20,5	25,8	1,0	680,0	27,3	71,3	21,3	12,4	0,3	0,1
Hokajärvi	8,6	180,0	2,0	5,8	1,7	2,2	67,8	4,0	8,6	10,6	0,8	336,7	8,8	77,6	20,2	2,5	2,7	0,5
Horkkajärvi	**22,9**	**75,0**	**1,3**	**5,6**	**0,8**	**0,8**	**225,5**	**6,1**	**22,9**	**27,8**	**0,4**	**580,0**	**17,0**	**67,7**	**18,9**	**4,1**	**0,3**	**0,4**
Hosiolammi	7,7	130,0	2,0	6,9	1,8	4,2	17,6	18,4	7,7	11,5	0,0	660,0	28,0	41,0	21,3	1,2	7,4	0,7
Iso valkjärvi (IVA)	**7,3**	**140,0**	**3,0**	**5,9**	**1,5**	**2,4**	**34,6**	**3,0**	**7,3**	**10,0**	**0,1**	**430,0**	**18,3**	**46,0**	**22,8**	**7,8**	**4,1**	**0,2**
Iso-Humalajärvi	12,8	270,0	3,0	6,3	0,7	1,2	74,2	4,6	12,8	13,4	0,2	540,0	12,7	66,9	20,6	2,3	3,6	0,4
Isojärvi	9,1	250,0		6,3	4,0	2,5	30,5	5,8	9,1	11,4	0,2	526,7	15,7	67,1	20,4	1,6	8,2	0,4
Iso-Valkee	2,4	830,0	6,5	8,8	3,4	0,5	1,3	1,4	2,4	2,5	0,0	190,0	7,2	15,0	18,2	0,7	662,9	0,2
Jylisjärvi	10,1	140,0		6,1	3,1	3,0	44,2	5,2	10,1	11,8	0,4	603,3	15,7	63,1	20,8	1,1	3,2	0,3
Kalliojärvi	22,6	80,0	2,3	6,0	1,1	0,6	222,3	4,4	22,6	26,8	0,4	590,0	14,0	62,6	15,8	6,0	0,4	0,3
Kernaalanjärvi	**12,8**	**70,0**		**10,4**	**4,8**	**10,2**	**75,1**	**53,0**	**12,8**	**13,9**	**0,6**	**736,7**	**61,0**	**100,3**	**18,3**	**5,6**	**0,9**	**0,9**
Keskinen Rautjärvi	12,8	130,0	2,3	6,7	1,5	2,7	112,1	11,1	12,8	14,3	0,6	493,3	20,3	75,6	21,6	2,7	1,2	0,5
Kylökkäänjärvi	18,4	130,0	1,5	5,9	1,1	0,9	147,2	8,7	18,4	21,1	0,2	546,7	15,3	59,6	20,1	4,5	0,9	0,6
Kyynäröjärvi	**17,8**	**55,0**		**6,6**	**9,5**	**10,6**	**116,1**	**21,2**	**17,8**	**20,1**	**1,3**	**1056,7**	**60,7**	**194,0**	**22,8**	**4,4**	**0,5**	**0,3**
Käkilammi	**33,5**	**60,0**		**6,4**	**38,1**	**4,3**	**314,0**	**37,9**	**33,5**	**36,9**	**1,0**	**1146,7**	**46,7**	**72,3**	**23,1**	**7,0**	**0,2**	**0,8**
Lapinjärvi	20,4	75,0		5,2	1,6	4,0	204,3	15,5	20,4	25,2	0,5	623,3	29,0	55,7	20,7	5,7	0,4	0,5
Latvajärvi	20,0	130,0	2,5	5,9	1,2	1,4	175,9	7,5	20,0	24,4	0,3	573,3	15,0	55,0	16,3	5,7	0,7	0,5
Leppälammi	24,7	65,0	1,3	6,0	1,3	3,0	249,1	30,8	24,7	29,2	1,1	693,3	30,7	65,0	22,8	7,8	0,3	1,0
Majajärvi	**23,4**	**70,0**	**1,5**	**5,8**	**1,3**	**1,8**	**235,9**	**11,0**	**23,4**	**28,0**	**0,5**	**710,0**	**33,3**	**61,3**	**18,8**	**7,7**	**0,3**	**0,3**
Mustalammi	20,7	80,0	2,0	8,4	2,7	3,1	198,2	17,2	20,7	25,7	0,4	660,0	27,7	36,2	18,0	7,4	0,4	0,6
Mustavirta	29,1	40,0		8,4	0,7	6,8	314,4	29,8	29,1	35,0	2,6	726,7	54,7	42,3	18,2	10,1	0,1	0,5
Onkimanjärvi	18,2	60,0	1,5	6,6	1,7	2,3	175,6	11,2	18,2	21,0	0,7	600,0	24,7	66,3	20,4	4,8	0,3	0,5
Oriharonjärvi	14,3	110,0		6,6	4,0	5,6	85,8	23,8	14,3	17,3	0,3	1130,0	47,7	131,3	21,8	8,1	1,3	0,5
Pannujärvi	9,3	230,0	2,5	6,1	1,2	2,3	49,7	5,5	9,3	10,8	0,6	463,3	14,3	72,0	21,4	2,0	4,6	0,4
Pikku Eläte	21,7	90,0	1,3	8,2	3,1	2,4	187,4	10,6	21,7	25,9	0,2	663,3	21,0	44,8	18,0	6,7	0,5	0,5
Pitkäniemenjärvi	13,5	110,0	2,0	6,3	1,7	1,4	130,5	7,0	13,5	14,8	0,6	456,7	15,3	60,6	21,5	4,2	0,8	0,5
Pursijärvi	6,9	300,0	4,0	6,8	2,0	1,7	12,4	2,3	6,9	6,8	0,1	393,3	9,2	155,2	21,2	1,1	24,2	0,2
Rahtijärvi	**15,8**	**115,0**	**2,3**	**6,3**	**1,7**	**1,7**	**148,3**	**9,8**	**15,8**	**19,5**	**0,5**	**546,7**	**18,7**	**69,0**	**20,1**	**4,0**	**0,8**	**0,5**
Rajajärvet-A	18,9	80,0	1,3	5,0	0,7	0,5	212,4	3,4	18,9	22,1	0,6	600,0	18,7	54,5	20,6	5,9	0,4	0,2
Rajajärvet-B	20,4	75,0	1,3	4,7	0,8	0,8	215,3	5,2	20,4	26,0	0,5	586,7	17,3	52,8	21,8	5,1	0,3	0,3
Rajajärvet-C	19,9	78,0	1,5	4,6	0,9	1,5	205,0	4,8	19,9	25,7	0,5	586,7	24,3	52,6	20,9	7,8	0,4	0,2
Ridasjärvi	14,7	80,0		6,5	13,2	8,1	94,5	13,0	14,7	17,1	0,6	526,7	36,0	126,5	19,6	3,4	0,8	0,4
Ruuhijärvi	17,2	85,0	2,0	5,8	2,1	3,0	160,6	28,5	17,2	20,2	0,6	696,7	46,3	61,1	20,2	6,3	0,5	0,6
Saloistenjärvi	7,6	280,0		6,5	2,2	2,0	15,5	4,6	7,6	9,0	0,1	580,0	11,7	75,0	20,6	1,4	18,0	0,4
Selkjärvi	6,2	290,0	3,8	5,5	0,9	1,1	27,0	3,6	6,2	7,4	0,2	330,0	9,5	47,0	20,0	2,8	10,7	0,4
Syrjänalunen	**2,9**	**400,0**	**4,3**	**5,7**	**1,0**	**1,0**	**4,4**	**2,5**	**2,9**	**3,2**	**0,1**	**196,7**	**7,2**	**81,0**	**19,0**	**3,2**	**91,7**	**0,3**
Tavilammi	14,4	80,0	1,5	6,6	1,3	2,3	113,3	7,7	14,4	18,1	0,1	620,0	20,0	56,0	19,7	3,2	0,7	0,4
Tervalammi	12,1	90,0	1,5	5,9	2,8	3,0	83,3	14,6	12,1	14,2	0,2	573,3	21,0	70,3	23,6	2,9	1,1	0,7
Tiponen	28,2	48,0	1,5	5,7	2,6	2,5	298,6	28,2	28,2	34,3	0,7	740,0	26,0	64,7	19,9	7,7	0,2	1,1
Valkea Mustajärvi	**5,4**	**450,0**	**4,5**	**7,8**	**0,9**	**0,9**	**13,8**	**4,3**	**5,4**	**6,5**	**0,0**	**370,0**	**8,9**	**50,7**	**17,1**	**1,0**	**32,5**	**0,5**
Vähä Humalajärvi	11,1	290,0	3,0	7,1	0,1	1,4	58,8	4,2	11,1	12,2	0,2	473,3	9,6	73,7	20,2	2,0	4,9	0,4
Vähäjärvi	5,8	350,0	3,0	5,6	63,7	0,9	29,0	2,5	5,8	7,5	0,2	353,3	8,8	48,6	20,5	5,2	12,1	0,3
Vähä-Koukkujärvi	23,4	130,0	1,5	5,8	1,0	1,0	209,1	5,7	23,4	27,4	0,3	543,3	18,3	72,3	15,4	1,5	0,6	0,3
Ylinen Rautjärvi	12,3	120,0	2,5	6,9	1,5	2,5	110,5	11,5	12,3	14,1	0,6	510,0	15,7	76,4	21,6	2,5	1,1	0,7

Appendix 2. Count, average body length (µm) and std deviation of Bosmina sp., Daphnia sp., Ceriodaphnia sp., Diaphanosoma sp. from SUSFISH (Haarajärvi-Majajärvi) and HUMI (Syrjänalunen-Käkilammi) data sets. The values from the SUSFISH data are averages from 2006-2013.

Data	Bosmina sp.		Daphnia		Ceriodaphnia sp.		Diaphanosoma sp.	
SUSFISH (n)	3211		3093		1423		366	
	mean	SD	mean	SD	mean	SD	mean	SD
Haarajärvi	310	±51	672	±177	370	±57	652	±143
Haukijärvi	351	±77	699	±178	433	±72	695	±114
Hokajärvi	303	±54	589	±139	408	±79	627	±136
Iso Valkjärvi_a	371	±83	577	±102	448	±90	585	±113
Iso Valkjärvi_m	344	±73	572	±157	429	±78	730	±106
Majajärvi	320	±64	654	±167	408	±78	667	±122
HUMI (n)	432		428		357		412	
	mean	SD	mean	SD	mean	SD	mean	SD
Syrjänalunen	210	±42	-	-	402	±73	650	-
Valkea-Mustaj.	245	±38	497	±117	377	±52	562	±117
Iso Valkjärvi_m	337	±81	419	±48	411	±65	552	±85
Kernaalanj.	316	±79	614	±181	-	-	542	±115
Rahtijärvi	279	±54	515	±99	369	±84	521	±78
Kyynäröj.	254	±49	421	±85	360	-	464	±69
Horkkaj.	362	±71	430	-	442	±58	516	±76
Majajärvi	306	±51	453	±67	355	±53	460	±118
Käkilammi	272	±79	480	±103	326	±58	507	±88

Appendix 3. Count of measured cladoceran genera in the HUMI sample. The "x" means that the genus was present in that lake.

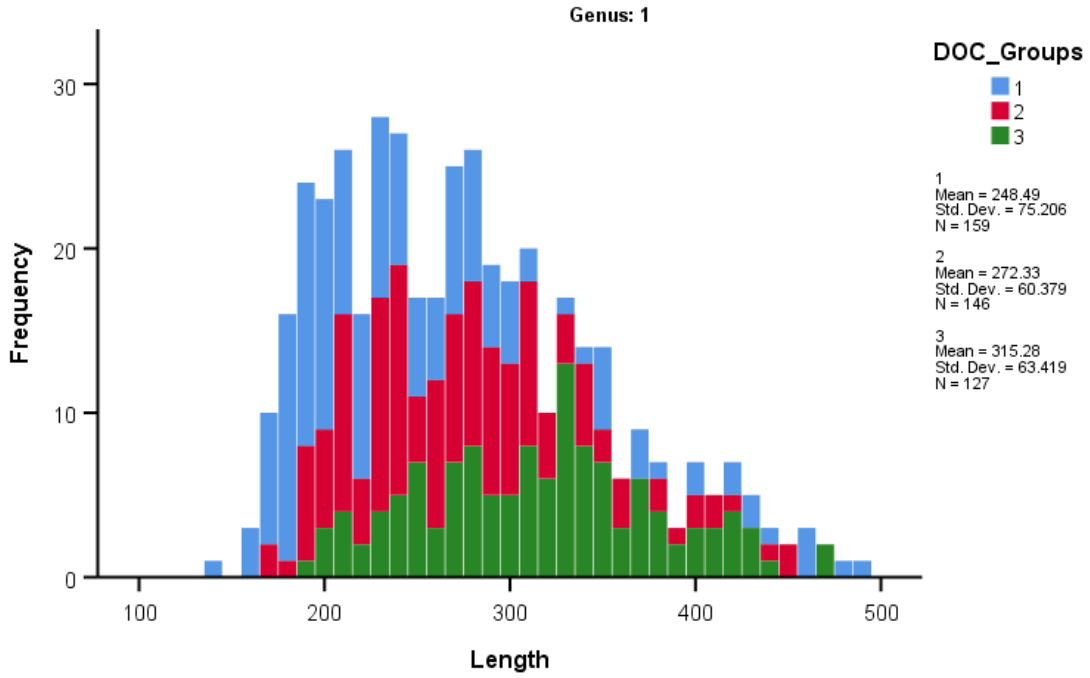
Genus	N	Syrjänalunen	Valkea-Mustaj.	Iso Valkj.	Kernaalanj.	Rahtijärvi	Kyynäröj.	Horkkaj.	Majajärvi	Käkilammi
Bosmina sp.	432	x	x	x	x	x	x	x	x	x
Daphnia sp.	428		x	x	x	x	x	x	x	x
Ceriodaphnia sp.	357	x	x	x		x	x	x	x	x
Diaphanosoma sp.	412	x	x	x	x	x	x	x	x	x
Chydoridae sp.	91				x			x		
Holopedium sp.	35		x	x						
Leptodora sp.	13		x				x			x
Polyphemus sp.	16							x		x
Sida sp.	1			x						
Limnosida sp.	7				x					
Alona sp.	1	x								
Scapholoberis sp.	4							x		
Bosmina_2	83				x					

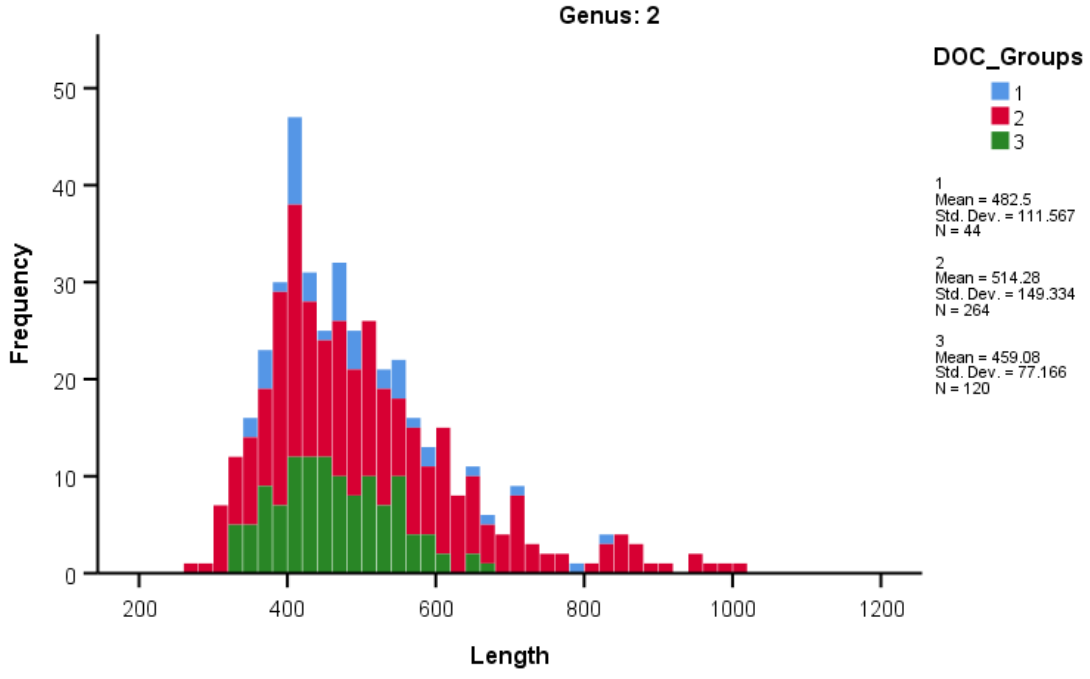
Appendix 4. Post hoc results from the cladoceran genera body length variance analyses in the DOC groups (ANOVA).

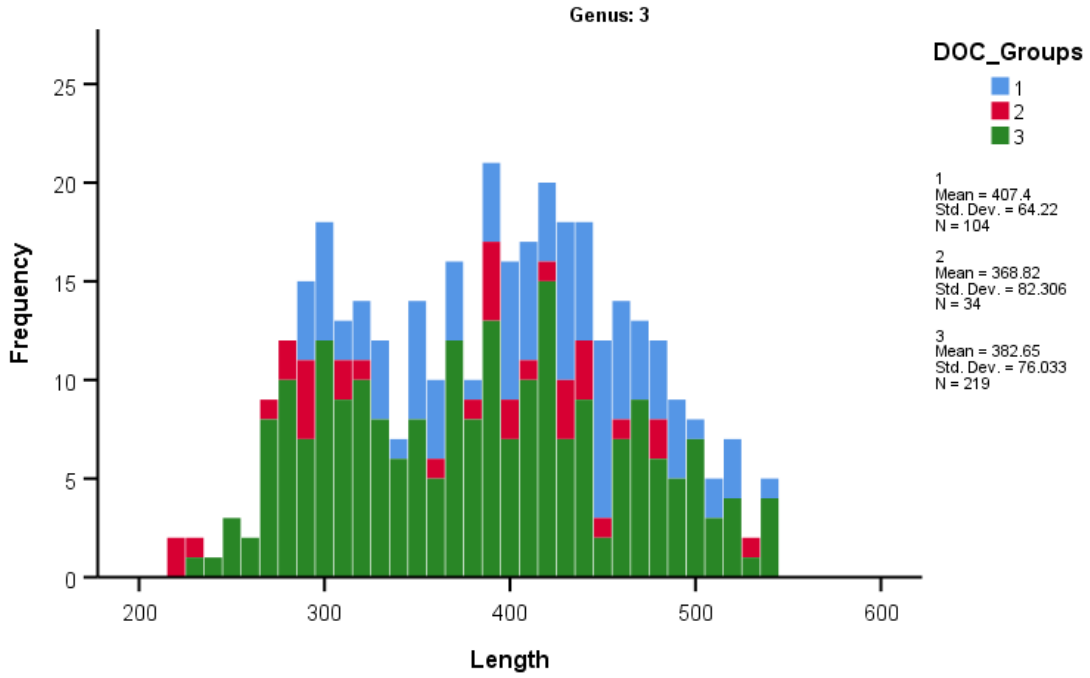
Data	Species	Post_hoc	DOC Groups	DOC Groups	Mean Difference	Std. Error	p	Confidence Interval (95%)	
								Lower Bound	Upper Bound
HUMI	Bosmina sp.	Tukey HSD	1.00	2.00	-23.838*	7.686	**0.006**	-41.92	-5.76
				3.00	-66.785*	7.98	**0.000**	-85.55	-48.02
			2.00	1.00	23.838*	7.686	**0.006**	5.76	41.92
				3.00	-42.947*	8.137	**0.000**	-62.08	-23.81
			3.00	1.00	66.785*	7.98	**0.000**	48.02	85.55
				2.00	42.947*	8.137	**0.000**	23.81	62.08
	Daphnia	Games-Howell	1.00	2.00	-31.78	19.167	0.228	-77.66	14.09
				3.00	23.417	18.235	0.41	-20.43	67.26
			2.00	1.00	31.78	19.167	0.228	-14.09	77.66
				3.00	55.197*	11.58	**0.000**	27.95	82.44
			3.00	1.00	-23.417	18.235	0.41	-67.26	20.43
				2.00	-55.197*	11.58	**0.000**	-82.44	-27.95
	Ceriodaphnia sp.	Games-Howell	1.00	2.00	38.580*	15.456	**0.042**	1.17	75.99
				3.00	24.755*	8.127	**0.007**	5.59	43.92
			2.00	1.00	-38.580*	15.456	**0.042**	-75.99	-1.17

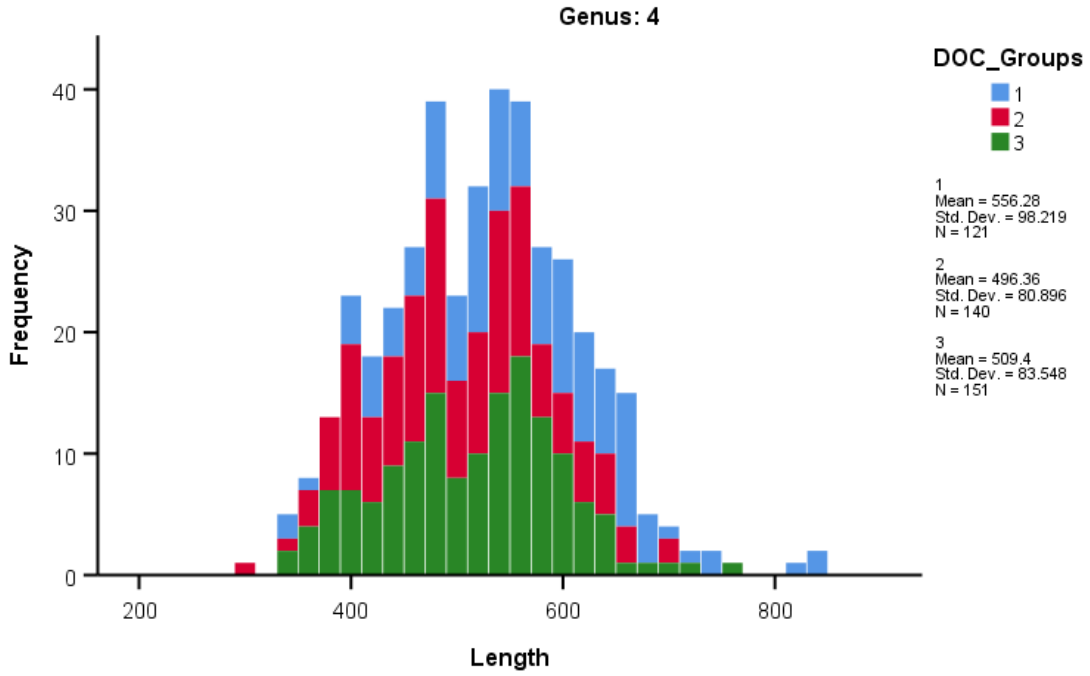
				3.00	-13.825	15.021	0.631	-50.31	22.66
			3.00	1.00	-24.755*	8.127	**0.007**	-43.92	-5.59
				2.00	13.825	15.021	0.631	-22.66	50.31
	Diaphanosoma sp.	Tukey HSD	1.00	2.00	59.924*	10.831	**0.000**	34.45	85.4
				3.00	46.877*	10.647	**0.000**	21.83	71.92
			2.00	1.00	-59.924*	10.831	**0.000**	-85.4	-34.45
				3.00	-13.047	10.238	0.41	-37.13	11.04
			3.00	1.00	-46.877*	10.647	**0.000**	-71.92	-21.83
				2.00	13.047	10.238	0.41	-11.04	37.13
SUSFISH	Bosmina sp.	Games-Howell	1.00	2.00	48.9619*	3.4775	**0.000**	40.8	57.124
				3.00	20.1165*	3.6109	**0.000**	11.643	28.59
			2.00	1.00	-48.9619*	3.4775	**0.000**	-57.124	-40.8
				3.00	-28.8455*	2.4762	**0.000**	-34.652	-23.039
			3.00	1.00	-20.1165*	3.6109	**0.000**	-28.59	-11.643
				2.00	28.8455*	2.4762	**0.000**	23.039	34.652
	Daphnia	Games-Howell	1.00	2.00	-53.9672*	8.1843	**0.000**	-73.184	-34.751
				3.00	-103.6338*	8.3888	**0.000**	-123.328	-83.94
			2.00	1.00	53.9672*	8.1843	**0.000**	34.751	73.184
				3.00	-49.6666*	6.5498	**0.000**	-65.026	-34.307
			3.00	1.00	103.6338*	8.3888	**0.000**	83.94	123.328
				2.00	49.6666*	6.5498	**0.000**	34.307	65.026
	Ceriodaphnia sp.	Games-Howell	1.00	2.00	40.5310*	8.2869	**0.000**	20.863	60.199
				3.00	27.3829*	4.8629	**0.000**	15.963	38.802
			2.00	1.00	-40.5310*	8.2869	**0.000**	-60.199	-20.863
				3.00	-13.1481	8.7718	0.294	-33.917	7.621
			3.00	1.00	-27.3829*	4.8629	**0.000**	-38.802	-15.963
				2.00	13.1481	8.7718	0.294	-7.621	33.917
	Diaphanosoma sp.	Tukey HSD	1.00	2.00	53.7989*	20.8125	**0.027**	4.819	102.778
				3.00	15.0815	21.5663	0.764	-35.672	65.835
			2.00	1.00	-53.7989*	20.8125	**0.027**	-102.778	-4.819
				3.00	-38.7174*	14.8142	**0.025**	-73.581	-3.854
			3.00	1.00	-15.0815	21.5663	0.764	-65.835	35.672
				2.00	38.7174*	14.8142	**0.025**	3.854	73.581

Appendix 5. Stacked histogram of the DOC groups (1. Low 2. Moderate 3. High) showing the measured body length (µm) distribution of the cladocera genera from the HUMI data. Genus: 1) Bosmina sp. 2) Daphnia sp. 3) Ceriodaphnia sp. 4) Diaphanosoma sp..






Genus: 3
Frequency
25
20
15
10
5
0
200
300
400
500
600
Length
DOC_Groups
1
2
3
1
Mean = 407.4
Std. Dev. = 64.22
N = 104
2
Mean = 368.82
Std. Dev. = 82.306
N = 34
3
Mean = 382.65
Std. Dev. = 76.033
N = 219


Genus: 4
Frequency
40
30
20
10
0
200
400
600
800
Length
DOC_Groups
1
2
3
1
Mean = 556.28
Std. Dev. = 98.219
N = 121
2
Mean = 496.36
Std. Dev. = 80.896
N = 140
3
Mean = 509.4
Std. Dev. = 83.548
N = 151